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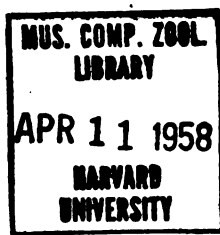


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# Heredity of Coat Characters in Guinea-Pigs and Rabbits

BY

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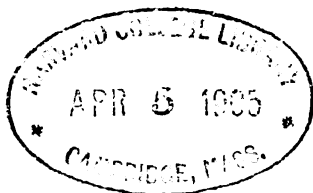


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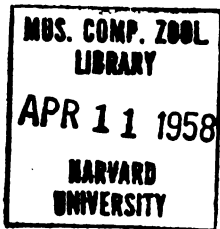
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# HEREDITY OF COAT CHARACTERS IN GUINEA-PIGS AND RABBITS.

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BY W. E. CASTLE.

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## INTRODUCTION.

The experiments to be described in this paper have been in progress in the Zoölogical Laboratory of Harvard University since the year 1900. They were begun for the study of conditions governing sex in the higher animals, but have yielded results bearing on certain other questions, which alone will be considered in this paper.

The animals used, guinea-pigs and rabbits, were selected because of their early maturity and fecundity. To provide them with food and shelter and to give them the necessary daily care, in addition to keeping records as full as possible, have been no small task. In this connection I am indebted for invaluable assistance to a number of persons. First of all to Prof. E. L. Mark, director of the zoölogical laboratory, without whose encouragement and support the experiments could never have been undertaken, and who has more than once come to the rescue when the material resources at my command were exhausted and further progress seemed impossible. The director and other officers of the Museum of Comparative Zoölogy, and the President of the University, have generously provided quarters for the animals and in other ways have aided the enterprise. Finally, when the increasing cost became a burden too heavy for the laboratory to bear, it was assumed by the Carnegie Institution of Washington in the form of a grant to Professor Mark and myself for experimental studies in heredity. Under the auspices of the Carnegie Institution the work has been in progress since January, 1904, and this paper is presented as a first detailed report upon it.

In the course of the experiments about 3,000 guinea-pigs and several hundred rabbits have been reared.

For valuable guinea-pigs and excellent practical suggestions I am indebted to Miss Jeannette Soule, secretary of the National Cavy Club; for an interesting stock of albino rabbits I am indebted to Prof. R. T.

Jackson. During the academic year 1903-1904, Mr. R. C. Kibbey has given me valuable assistance in the breeding experiments, and Mr. A. D. Howard in the study of the hair pigments.

### EXPERIMENTS WITH GUINEA-PIGS.

#### HEREDITY OF COAT COLOR.

In the coat of many mammals there occur two or more distinct pigments associated together in the same individual hair, and according as one or the other of these predominates in particular regions of the hair or of the body, a distinct "ticking" of the hair is produced, or a color-pattern of the body. Familiar examples of "ticked" or parti-colored hairs are those of mice, squirrels, and foxes. Body color-patterns of the sort mentioned occur in cats, tigers, leopards and the like.

In mice Bateson (:03)\* has shown that there occur three different pigments—black, chocolate, and yellow. In the wild mouse all these pigments occur together in the same individual hair, but in fancy mice the pigments may occur singly or combined in pairs, when they produce the color varieties most sought by fanciers. Bateson's observations have been confirmed by Allen (:04).

#### COAT OF THE WILD CAVY.

In wild guinea-pigs (or cavies) occur the same three pigments as in mice, viz, black, chocolate, and yellow. A skin of a young *Cavia aperea* Linn. from Brazil, which lies before me, shows a coloration similar to that of the "agouti" variety of the domesticated guinea-pig. On the back and sides of the body the ordinary hairs have a tip, about 2 mm. long, of a deep brownish-black color. Below this comes a yellow band of about the same length. The rest of the hair appears black, but is less heavily pigmented than the tip, and grows lighter toward its base, which is of a dull leaden color. Microscopic examination shows that the medulla of the hair, throughout its length, contains fine pigment granules of an intense black color, and associated with them others of a chocolate-brown color. The former are much more numerous than the latter, and both are much less abundant toward the base of the hair than at its tip. The cortex of the hair contains throughout the greater part of its length, where it is relatively thin, only some chocolate pigment with a very little black. But in the distal part of the hair the cortex is much thicker and more heavily pigmented. Its terminal 2 mm. has the combination of chocolate and black already described, but in the region just proximal to this it contains only bright yellow pigment, which produces the yellow ticking of the coat.

The longer, so-called contour hairs, found on the back and sides of

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\*The figures in parentheses refer to the Bibliography, p. 77.

the animal, are black throughout their length, lacking entirely the subapical yellow band. On the lower side of the body the hairs have a pigmentation similar to that of the ticked hairs of the back, but the yellow band is longer and less sharply limited, and the black tip is inconspicuous, so that the fur appears superficially of a dull yellow color, but when parted is seen to be leaden black at the base.

#### COLOR VARIETIES OF DOMESTICATED CAVY OR GUINEA-PIG.

In the various color varieties of domesticated cavy the same three sorts of pigment found in the wild animal exist singly or in combinations sometimes identical with those found in the wild animal, sometimes different.

##### AGOUTI.

In the *agouti* variety, of which there are two distinct sub-varieties, known respectively as golden and silver agouti, all three pigments are present, distributed as in the wild cavy. In the *golden* agouti the pigments of all three sorts are abundant and dark, so that the yellow band becomes a red of the sort found in a sorrel horse, while the remaining portions of the hair are fairly deep black. In *silver* agouti the pigmentation is less heavy. It may fairly be described as a dilute condition of the golden agouti. The yellow band is of a pale yellow color, and the black portions of the hair are a pale or bluish black. Silver agouti may be produced by crossing golden agoutis with albino animals of a particular sort, as will be explained presently.

##### YELLOW.

Yellow-coated varieties, with hair containing neither black nor chocolate pigment, are distinguished according to the depth of their color, as *red*, *yellow*, or *cream*.

In the lighter shades, as compared with the darker ones, the pigment granules are smaller and possibly less numerous. The *skin* covering the feet and ears of animals of this variety contains chocolate pigment, and, at least in some cases, black also; the eye, too, certainly contains chocolate pigment as well as black, yet the hair, as stated, never contains black or chocolate pigment.

##### CHOCOLATE.

Of the chocolate variety I have made as yet a very incomplete study, for lack of material. The two animals which I have had bore one a spot of red, the other a spot of yellow. Neither bore any black hairs. The chocolate hairs apparently contain no other pigment. Theoretically it should be possible to obtain a chocolate-colored animal entirely free from yellow as well as from black pigment, as is possible with mice (see Allen, : 04). My experiments have not progressed far enough to show whether this expectation can be realized.

## BLACK.

In the black variety, black pigment predominates over the other two sorts and obscures them. But I have never been able to obtain it in a pure state. Chocolate is invariably associated with it, and usually hairs can be found somewhere on the body which show the presence of the red-yellow pigment also.

In the ordinary black hair chocolate pigment predominates in the cortex, black in the medulla. I am unable to say whether the red-yellow pigment is present with them or not, but I am inclined to think that in some cases at least it is, for here and there on the body one can frequently find a hair devoid of the black and chocolate pigments, and such a hair commonly shows a red or yellow pigmentation. Still there are reasons for supposing that with proper attention a black variety could be produced which would have no red or yellow in its coat, just as red or yellow animals are obtained free from black and chocolate.

The black, like the red-yellow variety, occurs in forms more or less heavily pigmented, the lighter shades being known as *blue*. The latter can be produced by crossing black animals with red or yellow ones, or with albinos of certain sorts. Blue animals bear the same relation to black ones as silver agoutis to golden agoutis. Blue and silver agouti are *dilute forms* of black and golden agouti, respectively. In a blue animal the black and chocolate pigments are less abundant, and the red-yellow pigment, if it appears on separate hairs, is of a light (yellow) shade.

## ALBINO.

The albino or white variety, though apparently the simplest as regards pigment characters, is in reality the most complex. Albinos have pink eyes, the color of which is due not to a pigment, but to the blood seen through the transparent eye. The hair is likewise unpigmented at birth, and may remain of this character throughout life over the greater part of the body. Albino mice and ordinary albino rabbits apparently never develop pigment in any part of their coat, but such is not the case in caviae. Though I have carefully sought them, I have never yet seen albino individuals which in adult life did not form pigment in some region or other of their coat. This pigment makes its appearance first and chiefly at the extremities of the body—on the ears, the feet, and the nose—but may in extreme cases extend to the hairs of the body coat also. To the unaided eye the hairs of the extremities are of a sooty black color; the microscope shows them to contain chocolate pigment, with an occasional granule of black.

In the body hairs I have in one case identified reddish-yellow granules without those of other sorts. They are not at all abundant and are found principally at the tip of the hair, so that the coat looks like an

ordinary white one which has become dirty. For a long time I so accounted for the condition seen in a particularly unattractive albino in my flock, but finding that no change occurred in her coat, I investigated the case with the result noted. So-called Himalayan rabbits are albinos with peripheral pigmentation similar to that just described for cavies. But there occur also albino rabbits without peripheral pigmentation. In the Himalayan rabbit, as in the albino cavy, the coat of the young is commonly white at first all over the body, but soon becomes pigmented at the extremities. In some cases the first coat on the general body surfaces is slightly pigmented also, the pigment being found chiefly in the hair tip. This pigmentation is already forming at birth, and can be recognized by the deeper red color of the skin, as compared with that of normal individuals.

I have never seen a case in which this pigmentation of the hair-tips persisted in the adult animal, though that of the extremities regularly does. It is apparently in rabbits restricted to the first coat, though in guinea-pigs it is found only in the later coat.

It is difficult to formulate a satisfactory definition of an albino mammal. Absence of pigment is the most obvious characteristic of albinos; yet, as we have seen, many albinos possess a considerable amount of pigment. Furthermore, experiment shows that black-eyed white cavies, which produce no pigment whatever in the coat, nevertheless transmit very different hereditary pigment potentialities from those of albinos. Accordingly the *amount* of pigment produced in the coat is not distinctive between albinos and other animals; neither is the absence of pigment from the eyes distinctive, for Darbishire (: 04) has experimented with a race of pink-eyed mice which when crossed with albinos behave in every way like ordinary pigmented ones.

Without attempting a complete analysis of the matter, for which present knowledge does not suffice, I would suggest the following as criteria which, so far as observed, separate albino mammals sharply from all others. An albino is an animal with unpigmented eyes and with little or no pigment in its coat. The pigment, if present, is found in greatest amount *at the extremities of the body*. In a word, the pigmentation of an albino is essentially *centrifugal*. When by selection or cross-breeding the pigmentation is reduced, it is reduced centrifugally.

But in animals *not* albinos, the pigmentation is *centripetal*. Reduction of the pigmented areas takes place in this case toward well-marked centers, as has been pointed out by Allen (: c4) in the case of mice. From a study of spotted mice Allen was led to recognize for that animal five paired pigment centers situated dorso-laterally, as follows: (1) genal or cheek center, (2) nuchal or neck center, (3) scapular or shoulder center, (4) pleural or side center, and (5) sacral or rump cen-



ter. It is possible that we should recognize as a sixth distinct center the retina of the eye. These same centers are recognizable with great clearness in the guinea-pig, for in many cases adjacent patches, when not separated by unpigmented areas, contain elementary pigments whose limits are marked by sharp color contrasts. Thus a cheek patch may be black and the adjacent shoulder patch red (fig. 5) ; \* or the side patch black and the sacral patch red, or *vice versa* (figs. 1 and 3) ; or again, the right patch of a pair black, the left red, or *vice versa* (figs. 3 and 6). As compared with the mouse, the guinea-pig shows slight differences in the location and extent of the pigment patches, as one might expect

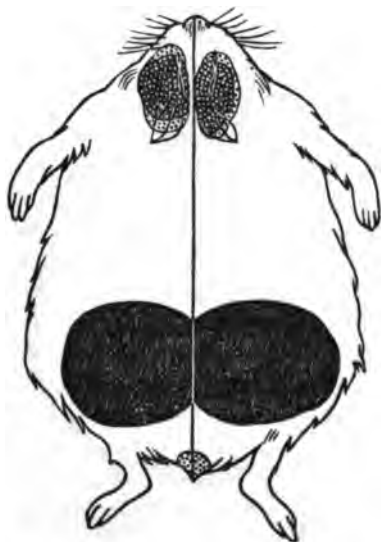


FIG. 1.—Diagram showing the coat pattern of ♀ 973. Cheek, side, and rump patches are present, though much reduced in extent. Each pair is of a different color.

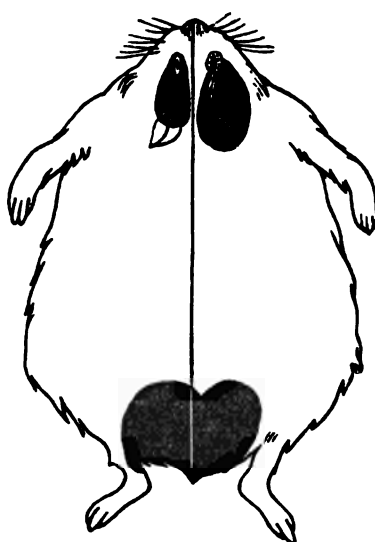


FIG. 2.—Coat pattern of ♀ 2166, a daughter of ♀ 973 (fig. 1). Cheek and rump patches are present, but no shoulder or side patches.

in forms structurally so different. The side patch of the guinea-pig lies chiefly posterior to the middle of the body and frequently extends well back, covering the greater part of the hip and hind leg, while the sacral patches may be so small and closely approximated that they seem to form an unpaired area at the extreme posterior end of the body (figs. 1, 5, and 7). The pigment patches are apparently not correlated with internal structures, such as the distribution of blood vessels or nerves. They are epidermal in origin and subject to more or less apparent asymmetry and mutual displacement, as if they were derived from distinct groups of ectodermal cells endowed in many cases with distinct pig-

\* In figs. 1-8, solid black indicates black coat; black stipple, red coat; white stipple on black ground, red and black hairs interspersed.

ment potentialities, which by unequal cell multiplication come to cover areas which may or may not be symmetrical in arrangement.

Sometimes one or both of a pair of patches is wanting altogether; in other cases a patch apparently gets displaced from its normal position, so that it lies across the median plane; frequently when a right or left patch is wanting, its mate extends somewhat beyond the median plane (fig. 3). Nevertheless, when one examines a number of spotted animals it is clear that there is a strong tendency for the pigmented areas to occur in the general body regions indicated, each of the ten recognizable patches being a unit in the composition of the coat.

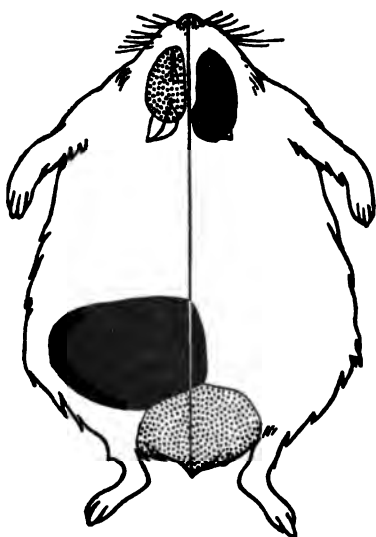


FIG. 3.—Coat pattern of ♂ 1358, a son of ♀ 973 (fig. 1). The right cheek patch is black, the left one red. There is a left side patch of black, but no right side patch. The fused rump patches are red.

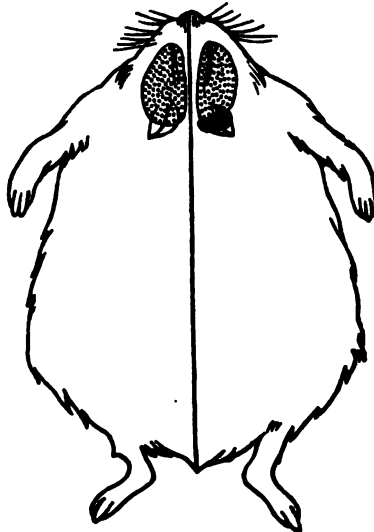


FIG. 4.—Coat pattern of ♂ 1360, a son of ♀ 973 (fig. 1). There are cheek patches of red, and a right neck (ear) patch of black. No others of the typical patches are present.

This unity may be obscured if it happens that two pigments, as black and red for example, are both present in the same patch. Nevertheless, in such cases one can often still identify the typical patches either by the occurrence of unpigmented areas between them, or by the occurrence of mixed pigments in one patch and of unmixed pigments in adjacent patches.

At one time I thought that I had obtained an explanation of the difference in behavior of the centrifugal and centripetal types of pigmentation. It seemed that the centrifugal pigmentation was of dermal origin, the centripetal of epidermal origin; but more careful examination of sections of the skin indicates that both sorts of pigmentation are similar in origin, arising within cells of the epidermis.

## SPOTTED.

The five principal color varieties of the cavy which have thus far been described are alike known as self-colored (*i. e.*, colored alike all over), in distinction from the spotted or pied varieties, which will next be noticed. Each of the four varieties, agouti, black, chocolate, and yellow (including red), may become spotted with white either by reduction in the extent of the pigment patches (as already explained), so that they no longer meet and cover the entire body, or by the entire absence of one or more of the typical color patches. The first-named process produces such familiar manifestations of partial albinism as (1)



FIG. 5.—Coat pattern of ♂ 2698. The cheek patches are of black, the combined neck and right shoulder patches red; in the corresponding area of the left side are a few black hairs mixed with the red; the side patches are black, the minute rump patch mixed red and black.

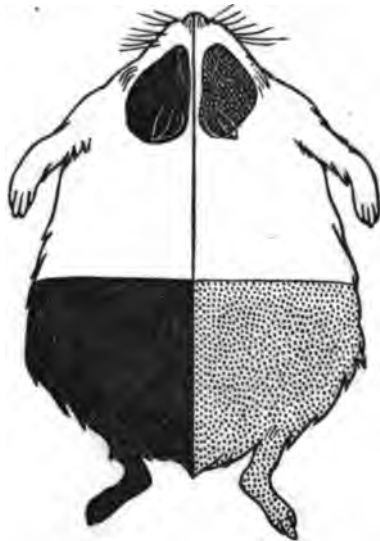


FIG. 6.—Coat pattern of ♀ 1920. The left cheek patch is black, the right one red and black mixed. The right side and rump patches are red, the left ones black. A sharp line of division separates them along the median plane both dorsally and ventrally.

a white spot or a longitudinal white streak on the belly of the animal, where the side or shoulder patches fail to meet below, or (2) a white throat, where the cheek patches fail to meet below, or (3) a white blaze (forehead stripe) where they fail to meet above (fig. 5), or (4) white feet, to which the shoulder and rump patches do not quite extend. Dropping out of one or more entire pigment patches may produce an asymmetrical white spotting, such as a white cheek, shoulder, or side. The two processes, reduction in extent of the pigment patches and dropping out altogether of certain pigment centers, usually progress simultaneously, and when they occur symmetrically may result in such

forms as the much admired Dutch-marked varieties, in which the two cheek patches are distinct (not united) above and below, the shoulder patches are wanting altogether, leaving a broad white girdle around the animal, and the rump patches fail to reach below the middle of the hind leg, though united dorsally (compare fig. 6, which shows an approximation to the Dutch-marked type).

A mottling similar in pattern, but with different color effects, is produced when the various patches are differently colored. Thus in one strain which I have bred from the beginning of my experiments, some of the pigment patches are usually pure black, others pure red, though

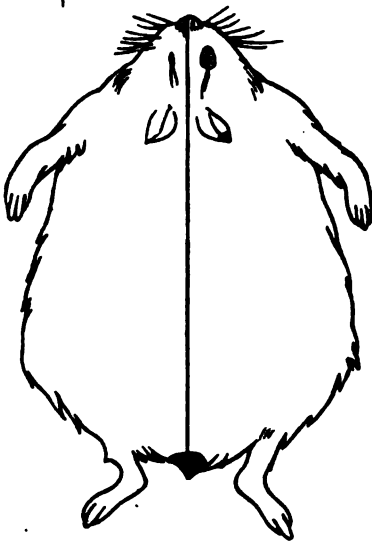


FIG. 7.—Color pattern of ♀ 2427. The color patches are of very limited extent. They consist of a red eye patch and a black neck (ear) patch in the right half of the body, and a median (paired, but fused?) rump patch.

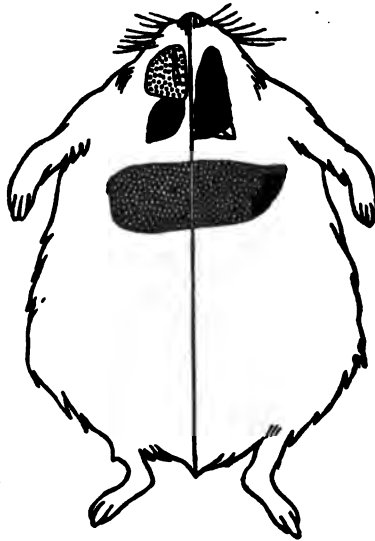


FIG. 8.—Color pattern of ♀ 2928. The left cheek patch is red, the adjacent neck (ear) patch black. The fused right cheek and ear patches are black. The fused shoulder patches are of mixed red and black.

occasionally a patch contains hairs of both colors intermingled. (See figs. 1-8.) Further, the patches in this strain frequently fail to cover the whole body, so that the animals are mottled with large clear areas of black, red, and white, a condition which undoubtedly has been common among domesticated cavies since their introduction into Europe from South America some three or more centuries ago. (See Cumberland, p. 11.)

#### BRINDLED.

In brindled animals black and red hairs are interspersed in the same pigment patches. The latter may or may not be continuous with each other; if they are not continuous, white mottling results, associated with the brindled character.

## ROAN, AND SILVERED.

In roan animals white hairs are interspersed with red ones. A similar modification may occur in the coat of black animals also, which are then said to be "silvered." I have never seen a cavy with an entire coat of this character; usually certain patches only are affected, or more often the ventral part only of a patch. I have noticed, however, the transmission of this character from generation to generation and have no doubt that a roan race or a silvered one could be established if desired.

## RESULTS OF CROSSING THE ELEMENTARY COLOR VARIETIES.

## ALBINOS AND PIGMENTED ANIMALS.\*

These two types are very distinct. Each by itself breeds true, and cross-breeding between them fails to produce intermediates; it results invariably in the production of young of the centripetally pigmented type. Thus in the course of these experiments, (1) albino parents mated *inter se* have produced 156 young, all albinos; (2) pure pigmented parents (*i. e.*, animals altogether devoid of the albino character) mated *inter se* have produced 261 young, all pigmented; and (3) albinos mated to pure pigmented animals have produced 314 young, all pigmented. The young produced by this last sort of mating, though similar in appearance to those produced by (2), are not *pure* pigmented animals, for they possess the potentiality to form albino young, which the young of the two pure pigmented parents do not. In Mendelian† terminology the pigmented character is *dominant*, the albino character is *recessive*, and cross-breds between a dominant and a recessive parent are *hybrid dominants*. The hybrids form gametes (*i. e.*, spermatazoa and eggs ready for fertilization), half of which, approximately, transmit the pigmented character, half the albino character.

Students of heredity at the present time are giving earnest attention to testing the two principles which make up Mendel's law, viz, (1) the principle of dominance, and (2) the principle of segregation. In the case under consideration there can be no question of the validity of both. The centripetal type of pigmentation invariably dominates over the albino, as the statistics already given clearly indicate. This is in harmony with numerous observations on mice, rats, rabbits, and other mammals made by Haacke ('95), Von Guaita ('98, :00), Cuénot (:03, :04),

\* Although, as we have seen, the albino guinea-pig regularly develops a certain amount of pigment in its coat, it will be convenient to use the term "albino" in contrast to "pigmented," the latter term referring only to the dark-eyed centripetally pigmented animals.

† For a brief statement of Mendel's law, see Castle (:03, or :03<sup>a</sup>); for a fuller one see Bateson (:02).

Darbishire (: 04), Castle & Allen (: 03), Bateson (: 03), Allen (: 04), and others. The evidence that segregation of the dominant and recessive characters occurs when the cross-bred pigmented animals form gametes is not less clear. The matter can be conveniently tested in two ways: (1) By mating a cross-bred with an albino animal, when half the young should be pigmented, the other half albino, if segregation occurs as demanded by Mendel's law; (2) by mating hybrids *inter se*, when we should expect three-fourths of the young to be pigmented, one-fourth albino. The first sort of mating has in these experiments produced 211 pigmented and 214 albino young, where the expectation is 212.5 of each sort, which certainly is a very close approximation. The second sort of mating has produced 264 pigmented and 112 albino young, the expectation being 282 pigmented and 94 albino young, *i. e.*, there are 18 more than the expected number of albinos in a total of 376 young, a fairly close approximation, but not so close as that observed in the first case.

Combining the results of all matings which are expected to produce albinos, we get the following:

	Pigmented.	Albino.
Expected.....	494.5	306.5
Observed.....	475	326

This shows an excess over expectation of 19.5 albinos in a total of 801 young, or about 2.5 per cent.

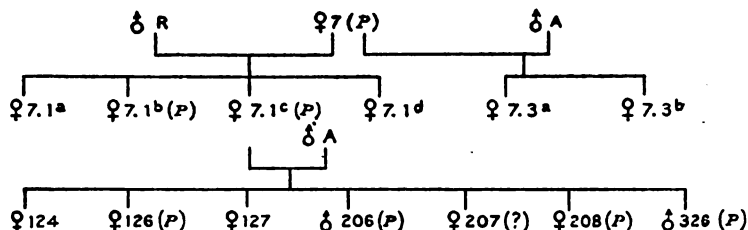


FIG. 9.—A genealogical table showing the character, as regards recessive albinism, of the young produced by three matings between a pure pigmented (*P*) and a hybrid pigmented animal.

Matings of hybrid pigmented with pure pigmented animals have, as expected, produced only pigmented offspring, which number 351. The Mendelian expectation is that half the young so produced will be *pure* in character, half *hybrid*. Since the two sorts look alike, only individual breeding tests will suffice to distinguish them. In certain cases such tests have been made, the results showing that the expectation based on theory is realized.

Fig. 9 shows the results of three different matings of this sort in a single

family of guinea-pigs. The animals enumerated were all pigmented; those marked (*P*), when mated with albinos, produced only pigmented young showing that they were *pure*; the others produced some albino offspring, when mated with albinos (or with other hybrid pigmented animals), showing themselves to be hybrid in character. In the case of one animal only (♀ 207) no test was made as to the production of albino gametes. This animal was paired with pure pigmented mates only, and the young were, of course, invariably pigmented.

It will be observed from fig. 9 that pure ♀ 7 was mated with two different hybrid males, viz, ♂ R and ♂ A. By ♂ R she had four daughters (♀ 7.1<sup>a</sup>, ♀ 7.1<sup>b</sup>, ♀ 7.1<sup>c</sup>, and ♀ 7.1<sup>d</sup>), two of them pure (*P*), two hybrid in character. By ♂ A she had two daughters (♀ 7.3<sup>a</sup> and ♀ 7.3<sup>b</sup>), both hybrid in character. In the next generation, hybrid ♂ A was mated with pure ♀ 7.1<sup>c</sup>, producing in three different litters seven pigmented young, which were used as breeders. One of these (♀ 207) was not tested for recessive albinism, as already stated. Of the others, four proved to be pure, two hybrid in character. Altogether there were among the young indicated in the table six pure individuals, six hybrids, and one of uncertain character.

So far as observed, there are no intermediate conditions between pure and hybrid pigmented animals. If an animal forms albino gametes at all, *half* its gametes are of that character. Of course in individual litters, or when only small numbers of offspring are dealt with, considerable deviations from the Mendelian ratios are likely to be encountered. This is to be expected on the theory of probabilities, as Allen (:04, p. 110) has clearly pointed out. But when more extensive tests are made the expected ratios are more closely approximated.

#### ALBINISM AND THE "LAW OF ANCESTRAL HEREDITY."

The foregoing results show very clearly that albinism conforms in its mode of inheritance to Mendel's law of heredity. The fact, however, must not be overlooked that a somewhat different explanation of its inheritance has recently been given, based on Galton's "law of ancestral heredity." I shall not at this time enter into a detailed discussion of Galton's hypothesis, which was an entirely rational one in the form in which it was originally proposed, and quite in harmony with the phenomena of gametogenesis as then interpreted. I have shown elsewhere (Castle, :03<sup>b</sup>) by a specific test in the case of mice, based on the observations of Von Guaita ('98, :00), that Galton's law fails to account for the observed facts concerning the inheritance of albinism, but that Mendel's law does this perfectly. Nevertheless Darbishire (:04), likewise dealing with albinism in mice, though admitting that certain of his results are not in disagreement with Mendel's law, is inclined rather

to interpret the phenomena on some such hypothesis as that of Galton. He states the matter very clearly (p. 24) as follows :

It is well known that according to this [Mendelian] view the hybrid contains equal numbers of germ-cells which produce the dominant character, and of those which produce the recessive; and this is said to be true of the hybrids however far the individual is removed from the original cross, whether it is the result of the cross (*i. e.*, the hybrid) or the great-great-grandchild of this. This is the ground on which the doctrine of the purity of the germ-cells and the law of ancestral heredity flatly contradict one another; the former asserting that  $DR \times DR$  will produce 25 per cent  $DD$ , 50 per cent  $DR$ , and 25 per cent  $RR$  for a very great if not an indefinite number of generations; the latter maintaining that the further the individual hybrid under consideration happens to be removed from the cross the less albinos will it produce; and that two hybrids whose mothers were albinos will produce more albinos than would two hybrids who have no albinos in their pedigree later than their great-great-great-grandmother. This seems to me to afford a case in which experiment could provide a decisive answer.

In this statement I heartily concur.

The experiment which Darbishire made was this. He made three different kinds of matings between animals which, we are told, were hybrids. (1) In one case each of the two animals mated had one albino and one pigmented parent. (2) In the second case, one animal was of the parentage just described, the other was born of two pigmented parents. (3) In the third case, the parents of both animals were pigmented. In brief, there were *two* albino grandparents in case (1), *one* albino grandparent in case (2), and *no* albino grandparents in case (3). The ancestry back of the grandparents was the same in all three cases. The conditions are thus very simple and should, as Darbishire suggests, give a decisive test. Darbishire states that—

	Number of young.	Number of albinos.	Albinos (per cent.).
Mating (1) gave.....	121	30	24.79
Mating (2) gave.....	107	20	18.69
Mating (3) gave.....	93	10	10.75

This is a seemingly conclusive demonstration of the correctness of Darbishire's contention; but in fact Darbishire's results, when carefully analyzed, prove just the opposite of his deduction.

Fortunately he has recorded in an appendix the various litters from which the totals given are made up. An examination of these records makes it evident that his so-called "hybrids" were not all hybrids. In mating (1) the animals used undoubtedly were hybrids, since each had, as stated, one albino and one pigmented parent. It is noteworthy that in that case the Mendelian expectation of 25 per cent albinos is



realized as perfectly as is possible in an odd number of young, there being 30 albinos in a total of 121 young. In cases (2) and (3) Darbishire gives us no evidence that the animals which he mated were really hybrids in the sense that they contained recessive albinism. He calls them "extracted hybrids" because they had dark eyes, as did all his *primary* hybrids obtained by crossing pink-eyed with albino mice. The latter unquestionably were hybrids in the sense that they contained recessive albinism, for in every case one of the parents was an albino. The former may or may not have contained albinism recessive; Darbishire's experiments indicate that in some cases they did, and in other cases they did not. Darbishire himself has shown that there is in his mice (contrary to an erroneous prediction of Castle & Allen, : 03, p. 612) no necessary correlation on one hand between recessive albinism and dark eyes, and on the other hand between freedom from albinism and the pink-eyed pigmented-coat condition. He calls especial attention to the fact (p. 22) that in five different families of his mice there occurred altogether seven pink-eyed pigmented animals, which in each case had one albino and one pigmented parent, and which accordingly must have been hybrids. In an earlier paper (Darbishire, : 03, p. 285) he showed that a pink-eyed mouse of this kind does produce albino offspring when mated to albinos, a thing which his original (pure) stock of pink-eyed mice never did. If, then, pink-eyed pigmented animals may contain recessive albinism, is it improbable that dark-eyed animals may in some cases *fail* to contain it?

Accordingly, in what have been called Darbishire's matings (2) and (3), we may reasonably ask for evidence that the animals mated were really hybrids. A pair which has produced albino offspring consists unmistakably of two hybrid animals. Pairs which fail to do this are questionably hybrid and may be provisionally left out of consideration. In mating (1) where both parents were unquestionably hybrid, since each had an albino parent, Darbishire gets the precise Mendelian proportion (one-fourth) of albinos. The question is, are fewer albinos produced by hybrids in matings (2) and (3), in which the albino ancestry was less.

Omitting only pairs which failed to produce *any* albinos in matings (2) and (3), Darbishire's observations may be summarized as follows :

	Pigmented young.	Albino young.	Albinos (per cent).
Mating (1).....	91	30	24.79
Mating (2).....	44	20	31.25
Mating (3).....	35	10	22.22
Matings (2) and (3) together.	79	30	27.52

Instead of producing *less* than 25 per cent of albinos, as Darbishire supposes them to do, matings (2) and (3) really produce *more* than that proportion of albinos. Considered separately they produce, one somewhat more than 25 per cent, the other somewhat less, as we should expect to be the chance result where small numbers of young are considered.

In further evidence that Darbishire's "extracted hybrids" did not in all cases contain recessive albinism, his matings of such animals with albinos are instructive (see his Table F, p. 36). Five out of nineteen such matings failed to produce *any albinos whatever*, though they produced a total of 19 young, all pigmented. If the pigmented parents in these matings had really been hybrids, half their young should have been albinos. Such was precisely the proportion of albinos produced by the fourteen matings in which the pigmented parent, though of the same ancestry as in the foregoing cases, showed itself to be really a hybrid, for these fourteen matings produced 36 pigmented young and 36 albinos.

Darbishire designates the cases just discussed "the most conclusive results which I have obtained" [in favor of the law of ancestral heredity]. Careful examination of these results, however, as we have seen, makes them seem far from conclusive in favor of that hypothesis. I have, therefore, thought it worth while to apply a further experimental test to Darbishire's hypothesis, in the case of guinea-pigs.

In doing so I class as a hybrid pigmented animal (1) any pigmented animal known to have had an albino parent, or (2) any pigmented animal born of pigmented parents which has produced one or more albino young. In Tables A and B are summarized the results of all of the matings between two animals known to be hybrids, or between a hybrid and an albino, which have been made in my later experiments. Matings from my earlier experiments are not included for the reason that the ancestry of the animals at that time used is too imperfectly known. The Mendelian expectation is, as Darbishire states, that all hybrids alike, whether they have few or many albino ancestors, will form gametes approximately half of which bear the albino character, half the pigmented character. Darbishire's contention, on the other hand, based on the hypothesis of Galton, is that the more albino ancestors a hybrid animal has, the more albino offspring will it produce. To test these alternative hypotheses I have tabulated the matings which have been made in these experiments according to the amount of albino ancestry involved in each, this amount being greatest in the first part of each table. Table A includes matings between two hybrids, Table B matings between a hybrid and an albino.

TABLE A.—*Proportions of albino young produced by hybrid pigmented parents of different amounts of albino ancestry.*

Albino grand-parents.	Albino great-grand-parents.	Albino young.	Pigmented young.	Remarks.
2	6	3	13	Two albino grandparents, 43 albino to 124 pigmented young, or 25.9 per cent. albinos.
2	4	9	28	
2	3	3	4	
2	2	11	28	
2	0	17	51	One albino grandparent, 16 albino to 18 pigmented young.
1	4	5	1	
1	3	3	4	
1	1	5	7	
1	0	3	6	No albino grandparents, 6 albino to 16 pigmented young.
0	1	1	3	
0	0	5	13	
...	...	65	158	

TABLE B.—*Proportions of albino young produced by matings between albinos and hybrid pigmented animals, both with varying amounts of albinism in their ancestry.*

Albino grand-parents.	Albino great-grand-parents.	Albino young.	Pigmented young.	Remarks.
3	7	1	3	Three albino grandparents, 55 albino to 64 pigmented young.
3	6	24	35	
3	5	5	6	
3	4	10	9	
3	3	4	2	
3	2	3	1	
3	1	3	1	Two albino grandparents, 63 albino to 56 pigmented young.
3	0	5	7	
2	6	1	3	
2	5	8	3	
2	4	21	20	
2	3	8	8	
2	2	16	15	One albino grandparent, 13 albino to 18 pigmented young.
2	0	9	7	
1	5	0	3	
1	2	4	3	
1	1	2	3	
1	0	7	9	
0	3	2	4	No albino grandparents, 5 albino to 10 pigmented young.
0	0	3	6	
...	...	136	148	

Throughout Table A we find the expected Mendelian ratio (1 : 3) of albino to pigmented young approximated, quite irrespective of the amount of albino ancestry back of the parents mated. Of course, there are marked deviations in individual cases where the number of young

is small, as we expect on the theory of probabilities, but we find no falling off in production of albinos as the amount of albino ancestry decreases.

Similarly throughout Table B we find the expected Mendelian equality of albino and pigmented young approximated, irrespective of the number of albino grandparents and great-grandparents. Thus the proportion of albinos is actually higher when there are only two than when there are three albino grandparents, though on Darbishire's hypothesis we should expect this relation to be reversed; for the young produced in cases where there are *three* albino grandparents aggregate 55 albino to 64 pigmented animals, an excess of 4.5 pigmented; but the young produced in cases where there are only *two* albino grandparents (in the same total number of young) aggregate 63 albino to 56 pigmented animals, an excess of 3.5 albinos. The deviations from equality are in the two cases opposite in character and almost equal. Undoubtedly it is merely a chance outcome that they are opposite in nature to what Darbishire's hypothesis demands. The tables as a whole, however, do give an emphatic negative to Darbishire's position. They lend support to the alternative (Mendelian) hypothesis, that any pigmented animal which forms albino gametes forms approximately 50 per cent of such gametes.

In what precedes I have made no mention of what has been called Pearson's modification of Galton's law of ancestral heredity. Elsewhere (Castle, : 03<sup>b</sup>) I have discussed this briefly in applying a statistical test to the laws of Galton and Mendel in the case of albinism in mice. Galton's law I applied generation by generation to Von Guaita's ('98, : 00) mouse records, as Galton ('97) himself had applied his law to the Basset hound records. The test thus made showed the complete failure of Galton's law as applied to the heredity of albinism. No such detailed test was made in the case of Pearson's law, but the statement was made: "Comparing Pearson's series with that of Galton we see that the parental influence is reckoned as substantially the same by both Galton and Pearson, but that Pearson assigns a much greater influence to the more remote ancestors than does Galton." For which reason it was concluded, "The discrepancies noted between observed and calculated [in testing Galton's law] will remain and even be accentuated if we replace Galton's series with one of those suggested by Pearson. For the result will be unchanged [I should have said similar, rather than unchanged] in Generation II, but the calculated numbers will in most cases diverge still more from the observed ones, in the later generations, because Pearson attaches more weight to the remoter ancestors than does Galton." To these conclusions Pearson (: 04) takes exception, maintaining that neither of the two series which I took from his writings was quoted in a form comparable with that of Galton's series.

He gives a series of his own and that of Galton in comparable form. They are, he says, "if we measure parental influence by intensity of correlation":

Influence.	Pearson's series.	Galton's series.
Parental.....	$\frac{1}{2}$	$\frac{1}{2}$
Grandparental.....	$\frac{1}{4}$	$\frac{1}{4}$
Great-grandparental.....	$\frac{1}{8}$	$\frac{1}{8}$
Great-great-grandparental....	$\frac{1}{16}$	$\frac{1}{16}$

Even when they are given thus, it seems to me still, as I stated before, that "Pearson attaches more weight to the remoter ancestors than does Galton," and if so, that "the discrepancies noted between observed and calculated [in testing Galton's law] will remain and even be accentuated if we replace Galton's series with one of those suggested by Pearson." That Pearson himself had not contemplated such a test of his law would not affect in the slightest degree the outcome of the test. Further, it seems to me an admission very damaging to a law of heredity when Pearson says: "Personally I have no means of determining whether the law of ancestral heredity holds or does not hold for coat color in mice. The theory has not yet been worked out in a form covering Von Guaita's cases." Yet in Von Guaita's material we have a full record of the coat color of every animal in seven successive generations, and we know that back of this for an indefinite number of generations all the ancestors on one side of the ancestry were albinos, on the other side spotted black-and-white. That is sufficient basis on which to make very reliable predictions as to the character of the offspring, under Mendel's law, as I have elsewhere shown.

In fact, it seems to me that Pearson's law, as he now explains it, is *not a law of heredity at all*, but one of variability in successive generations, for he says (p. 110): "So far as I can understand the Law of Ancestral Heredity as I have myself enunciated it, the produce of a grey mouse and a fawn mouse might be on the average a green mouse without that Law having anything to say on the point. From it you can not possibly deduce what number of the offspring of any generation will be like this or that ancestor. It is not a law of types, but of the distribution of deviations from type, and this is a very different thing indeed." But from a genuine law of heredity, such as that of Mendel, one is enabled, as I have shown, to predict with great accuracy what color types will prevail among the offspring in successive generations. Since Pearson's law, as now interpreted by its author, though dealing with alternative color types in successive generations, gives no informa-

tion whatever as to *what* color types will prevail in one as compared with another, nor as to what proportion of the young will be *devoid* of color, it would seem desirable, to avoid confusion, that the law be re-named as something other than a law of heredity.

#### ALBINISM AND SEXUAL PREPOTENCY.

Galton ('97), on purely empirical grounds, was inclined to think the male sex prepotent in the transmission of black spots in the case of Basset hounds. Though I have elsewhere (Castle, :03<sup>b</sup>) shown that the conclusions which he drew from that study were probably erroneous because they rested on false assumptions, it may be worth while in this connection to test the idea of sexual prepotency in regard to albinism. This may be done by comparing the results of reciprocal matings, as shown in Table C, which contains a summary, as regards the production of albino young, of most of the matings made up to this time. Only matings between pigmented parents of undetermined character as regards recessive albinism have been omitted from this summary. These omitted matings produced several hundred young, all pigmented, as was to be expected if either one or both pigmented parents were free from recessive albinism. From Table C it is evident that, (1) when a mating is made between a hybrid pigmented and a pure pigmented animal the result is the same whether the hybrid be father or mother; in every case the young are pigmented; (2) when a mating is made between a hybrid pigmented animal and an albino, hybrid pigmented and albino young are produced in approximately equal

TABLE C.—*Proportions of pigmented (p.) and albino (a.) young produced by matings of various sorts.*

Mothers.	Father pure pigmented.	Father hybrid pigmented.	Father albino.
	Young.	Young.	Young.
	p. a.	p. a.	p. a.
Pure pigmented.....	261 : 0	215 : 0	205 : 0
Hybrid pigmented .....	136 : 0	264 : 112	120 : 116
Albino.. .....	109 : 0	91 : 98	0 : 156

numbers, viz, 120 pigmented to 116 albino young when the albino parent was a male, 91 pigmented to 98 albino young when the albino parent was a female. The deviations from equality are very slight and unquestionably the result of chance. In the one case the deviation is 2 individuals in a total of 236; in the other, it is 3.5 in a total of 189 young. There is, accordingly, in this case no evidence of prepotency in the transmission of albinism on the part of either sex.

## ALBINISM AND LATENT PIGMENT CHARACTERS.

Although, as we have seen, (1) albinism is a condition recessive in heredity with respect to ordinary or centripetal pigmentation, and (2) albinos produce only albino offspring, irrespective of their ancestry, it is not true, as might be supposed, that one albino breeds like another when *crossed* with the same centripetally pigmented type. This matter has been very fully discussed by Allen (:04, p. 130), but may be illustrated by some simple examples. (1) My albino guinea-pig, ♂ 2002, when mated with red females, invariably produces offspring marked with *black* as well as with red pigment. (2) Albino ♂ 635, when mated with the very same or with similar red females, produces young about half of which are pigmented with black and red, like the offspring of ♂ 2002, the other half being pigmented only with red or yellow, not with black. (3) Albino ♂ 1999, when mated with red females, produces only red (or yellow) pigmented offspring, never black pigmented ones. From an inspection of these three albino males or of their offspring by albino females, one would get no inkling of the existence among them of the differences revealed by the experiment described. This experiment shows that in the gametes produced by ♂ 2002, the capacity to form black pigment is latent. This capacity is exercised whenever such a gamete unites with one bearing the centripetal type of pigmentation. In ♂ 635 only about *half* the gametes formed contain latent black; in ♂ 1999 *none* of the gametes formed contain latent black. The idea underlying this explanation is that a recessive character (in this case albinism) may contain the dominant one (centripetal pigmentation) in a state of inactivity which nothing but cross-breeding with the pigmented type will disturb. Further evidence in support of this idea will be adduced when we come to discuss coat characters other than those of pigmentation.

Meanwhile, let me say a word concerning the term *latency*. In common with others I have frequently in earlier papers used this word loosely as synonymous with recessive. This usage was, I believe, an unfortunate one; accordingly, in what follows I shall use the two terms for conditions quite distinct, which my experiments show to have a real existence and to require names. (1) *Recessive* I shall use as Mendel used it, to designate a character which disappears when brought by fertilization into the same (hybrid) individual with a contrasted "dominant" character, but which is transmitted, distinct from the dominant character, in half of the gametes formed by the hybrid individual. (2) *Latency*, as I shall use it, is a condition of inactivity in which a normally dominant character may exist in a recessive individual or gamete. It is questionable whether a *recessive* character

may ever be latent. Future investigations alone can decide this point. A *recessive* character apparently reappears pure in half the gametes formed by the hybrid dominant individual, and is present in *all* the gametes formed by a recessive individual; a *latent* character apparently *never* regains its existence apart from the recessive (*i. e.*, becomes active) until cross-breeding brings this about. Future investigations may require further modification or even entire abandonment of these definitions, but for the present I find them useful to express the results of my experiments.

Latency of pigment characters in albinos is particularly clear in mice, as shown by the investigations of Cuénot (:03), Darbishire (:04), and especially of Allen (:04). For albino mice are, so far as known, wholly unpigmented, yet they ordinarily, perhaps always, transmit latent pigment characters, either singly or in combinations identical with those occurring in pigmented mice. Alike in guinea-pigs and in mice, a clue to what pigment characters are latent in the individual may often, though not always, be learned from a mere knowledge of its parentage. Thus, in guinea-pigs, an albino born of two red or yellow parents does not transmit latent black in any of its gametes; but one born of two black parents may or may not form gametes transmitting red apart from black pigment. The reason for this difference will be apparent when we come to consider the relation of red and black to each other in cross-breeding. For the present I would merely call attention to this case as showing that it is not the *ancestry* of the albinos which governs the behavior of their gametes in cross-breeding, as Darbishire (:04) maintains, but rather the existence of pigment characters as distinct entities, though latent, in the gametes formed by albinos. In certain cases we can, with confidence, predict the absence of a pigment character, even in a latent condition, from the gametes of an albino, viz, in cases where we know the pigmented parents to have been free from that character. Thus an albino born of red or yellow parents does not transmit black, because red or yellow animals do not contain the black character either active or latent, and so can not transmit it to their albino offspring. Where the parentage is unknown, suitable breeding tests show with equal certainty (often the production of as few as two young indicates clearly) what latent pigment characters are transmitted by the albino. A particular pigment character, when present latent in the gametes formed by an albino, appears to be regularly present either (1) in *all* the gametes formed, or (2) in *half* those formed, as suggested by the cases of albino ♂♂ 2002 and 635 already cited. No evidence exists of the occurrence of a latent pigment character in other proportions of the gametes, as should be the case on the "ancestry" idea of Darbishire.



## INTERCROSSING OF DIFFERENT PIGMENT TYPES.

Intercrossing of elementary pigment types other than albino results not in perfect dominance of one and complete disappearance (recessiveness) of the other, but in coexistence of the two in the offspring, though one pigment character from its nature may be much more in evidence than the other. Thus black animals mated with red ones ordinarily produce black offspring, though of a shade different from that of the black parent, the more intense black pigment masking to a great extent the presence of red. True Mendelian dominance, then, is wanting in such crosses; nevertheless the other Mendelian principle, segregation, is here realized.

## THE AGOUTI TYPE.

An agouti animal, as we have seen, is one which bears the three pigments—black, chocolate, and red-yellow—in a particular regional distribution on the same hair. It is the original or wild type of pigmentation and might be expected to show superior potency in crosses. My experiments, which, however, are far from complete, indicate that this type of pigmentation as transmitted in the gametes of a wild animal really is potent over other types. Thus, a male *Cavia aperea*, which was captured wild in southern Brazil, has produced by two different domesticated albino females (neither of which was of agouti-colored parentage) 15 young, all agouti-colored, but in some cases at least of a somewhat lighter shade than the wild parent. I can not speak very emphatically as to the exact shade of pigmentation in several cases, because all but four of the hybrids were born dead, and their coats have been examined as yet only in a wet condition. This matter will be discussed more fully in a subsequent paper.

The agouti type of pigmentation, when borne by gametes of a domesticated guinea-pig, likewise shows a strong tendency to dominate over other types of pigmentation, the only possible exception thus far observed being black.

*Agouti* × *agouti*.—It goes without saying that pure agoutis, like pure\* animals of any other type, breed true. Thus, agouti ♂ 2017 mated with agouti ♀ 2019 and 2021 produced 6 young, all of the same (golden) agouti type as the parents.

*Agouti* × *black*.—Agouti ♀ 2018 mated with black ♂ 2053 (known by test to be pure) produced 3 young, of which one was an agouti, the other two black. This outcome indicates that the black type of pigmentation may in some cases at least have equal potency with the

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\* The term *pure* is here used, as throughout this paper, in the Mendelian sense, referring to the character of the gametes which an animal forms. Thus a pure agouti animal is one which forms gametes all of which transmit the agouti type of pigmentation.

agouti, showing *alternative* dominance with respect to it. When this result was obtained I at once questioned the purity of ♀ 2018, suspecting that she might contain recessive black, but her purity has since been established with considerable probability by a mating with albino ♂ 635, neither of whose pigmented parents was an agouti. This mating produced 4 young, all agouti or agouti spotted with red. Previously ♀ 2018 had been mated with agouti ♂ 2017, producing 3 agouti young.

Further support for the idea that agouti and black may show *alternative* dominance is afforded by matings of hybrid agouti (albino)\* ♀ 2020. This animal contained recessive albinism in which black apparently was latent. For, when mated with agouti ♂ 2017, she produced 2 agouti and 2 black young, indicating that at least half her gametes bore the black character, and that this dominated over agouti in at least two out of four cases. When mated with albino ♂ 2039 she produced 1 albino, 1 spotted white >† red-black, and 1 spotted red-black young. Mated with hybrid red (albino) ♂ 1019, she produced 2 black > red young. Manifestly only part, if any, of this female's gametes bore the agouti character, though all apparently bore the character black, either in the agouti combination or in the segregated state.

Again, an agouti daughter of ♀ 2020 by agouti ♂ 2017, viz, agouti (black?) ♀ 1035, when mated with albino ♂ 2059, produced 2 agouti > red, and 2 black > red young. This result indicates that ♀ 1035, like her mother, formed gametes, half only of which bore the agouti character, half the black character. But the black character is apparently present in ♀ 1035 as a simple recessive, not latent in recessive albinism as in her mother; for the mating of ♀ 1035 with albino ♂ 2059, though it produced 4 young, gave no albino offspring; and a subsequent mating with white > red-black (albino) ♂ 1631 likewise gave no albino offspring, but 1 agouti and 1 black-red young. This ♀ 1035 undoubtedly arose from the union of an agouti gamete furnished by the father (since he was shown by breeding tests to be pure) with a gamete bearing the black character furnished by the mother, ♀ 2020. But if ♀ 1035 does not contain recessive albinism, the gamete furnished at her formation by ♀ 2020 can not have been an albino gamete. It would seem then that ♀ 2020 furnished certain gametes bearing black, not latent in association with albinism, but active. If so, she must have borne two different pairs of contrasted pigment potentialities, viz, (1) centripetal pigmentation *vs.* albinism; (2) agouti pigmentation *vs.* black pigmentation; and she must have transmitted

\* A character indicated thus in parentheses is present in a *recessive* condition.

† This symbol is used to indicate inequality in the extent of body areas of different character as regards pigment. Thus, white > red means an animal with more white than red fur on its body.

centripetal pigmentation associated either with agouti or with black pigmentation (for the latter combination ♀ 1035 is specific evidence), and albinism associated probably either with agouti or with black pigmentation (these of course being in a latent condition). It seems from this and other similar cases that *the regional distribution of pigments on the body* (centripetal *vs.* albino) *is something inherited independently of the specific character of the pigments formed.* Albinism *vs.* centripetal pigmentation forms one pair of alternative (Mendelian) characters; agouti *vs.* black pigmentation forms another pair. An animal like ♀ 2020, then, is a dihybrid as regards pigment characters, and should form in equal number gametes of four different sorts, viz, albino [black latent],\* albino [agouti latent], centripetal agouti, and centripetal black. This idea is supported by Allen's (: 04) observations on mice, and finds frequent illustrations in these experiments.

*Agouti* × *red*.—I have made this mating between pure parents only once. Agouti ♀ 2019, mated with red ♂ 2054, produced 4 young, 3 of them agouti > red, 1 red > agouti > white. This result indicates a tendency of agouti to dominate over red, or at least to mask the presence of red. In this experiment, the mother, ♀ 2019, had a red hip patch. The occurrence of red and of white spots on the young was probably due to a mosaic character of certain of her gametes rather than to some peculiarity of the father, a self red.

One of the young produced by this cross, viz, agouti > red ♀ 1294, when mated with her red father, ♂ 2054, produced 6 young, 2 agouti > red, 1 red > agouti, 2 red-black, and 1 red, indicating segregation of the respective agouti > red, and red characters brought together in the previous generation, so as to allow of the formation of pure red gametes. The occurrence of two red-black young indicates that in some cases the agouti character may break up into isolated black and red under the influence of the cross.

*Agouti* × *albino*.—Pure agoutis mated with albinos of spotted or of unknown ancestry have produced only animals predominantly agouti-colored, though the offspring have in some cases had one or more of the typical color patches red or white, but never black or chocolate. The spotting with red or white was inherent in the agouti stock used.

It is probable that in no case did the albino parent in these crosses transmit latent agouti. This statement is based on the results of other crosses made with these same albino animals, as well as on an examination of their pedigrees. If this assumption is correct, there is seen in this experiment a strong tendency for the agouti character to dominate over other pigment characters contained latent in albino gametes; for every one of the 17 young was agouti-pigmented.

\* Brackets will be used to indicate latent characters, just as parentheses to indicate recessive ones.

The matings made and their results are :

Parents.		Young.			
Gold. agouti.	Albino.	Agouti.	Agouti-red.	Agouti red-white.	Silver agouti-yellow-white.
Agouti ♀ 1030 .....	♂ 635.....	2	3	..	...
Agouti > red ♀ 1029	♂ 2059...	...	3	...	...
Agouti ♀ 2017.....	♀ 785.....	3	1	...	...
Agouti ♀ 2018.....	♂ 635.....	1	2	1	...
Agouti > red ♀ 2021.	♂ 635.....	...	...	...	1
Total.....	.....	6	9	1	1

That an albino may transmit latent agouti is shown unmistakably by the following case. Albino ♂ 2060 was purchased from a breeder and his ancestry is wholly unknown to me. But I found on mating him with spotted females not of agouti parentage that a large proportion of his young were agouti-marked, and this proportion proves to be almost exactly one-half. Thus he has produced by 15 different females, which were spotted with black and red (and in some cases also with white), 19 young marked with agouti (in no case with solid black hairs on the body, though frequently with red or white ones) and 18 young marked with black but not with agouti. By the red or red-white females he has produced 3 agouti-marked and 3 black-marked young. The total pigmented young produced by matings with the spotted females are 22 agouti-marked and 21 black-marked, an approximation to equality as close as is possible with an odd number of young. The matings with red and red-white females show that all the gametes formed by ♂ 2060 bear the latent character black pigmentation, but that half his gametes transmit it in the agouti combination with red, half in the form of solid or segregated black.

If this interpretation is correct it should be possible by suitable matings of ♂ 2060 with his descendants, or of the latter *inter se*, to obtain albinos *all* of whose gametes would transmit latent agouti. This matter, it is hoped, can soon be given an experimental test.

In the foregoing case it seems necessary to assume the dominance of agouti pigmentation over the intermingled condition of black and red spots; indeed, all my experiments support that idea, except possibly those mentioned in discussing the agouti × black cross (p. 26). The alternative dominance which may have occurred in those cases is apparently exceptional, the rule being that agouti pigmentation dominates over black or black-red. Alternative dominance can scarcely be invoked to explain the results obtained from the matings of ♂ 2060, for it would fail to account for the black-red offspring in the matings with red or red-white females.

The following experiment likewise bears upon the point which is under discussion. Agouti ♂ 2017, mated with albino ♀ 785, produced 3 agouti and 1 agouti > red young (as stated on p. 29). The albino ♀ 785 was born of albino parents, but part of her grandparents and great-grandparents were spotted black-red-white, part of them albinos; none were agouti-marked. It seems probable, therefore, that the pigment characters latent in the gametes of ♀ 785 were in every case black-red. If so, her agouti young should contain recessive white with which black-red had been introduced as a latent constituent, and should, as explained on page 28, form in equal numbers gametes of four sorts, viz, agouti, black-red, albino [agouti latent], albino [black-red latent]. If two such sets of gametes be combined (as in mating these hybrid young), and all gametic unions prove equally fertile, their young should be, on the hypothesis that agouti is dominant over black-red, in the proportions 9 agouti to 3 black-red to 4 albino; but on the hypothesis that agouti and black-red are alternatively dominant, the young should be in the proportions 6 agouti to 6 black-red to 4 albino. That is, on one hypothesis, agouti young should be three times as numerous as black-red; on the other hypothesis, both sorts should be equally numerous. The result observed is 7 agouti to 3 black-red to 3 white, which certainly favors the hypothesis that agouti dominates over black-red, though the number of young is undesirably small.

The details of the experiment follow :

Parents.	Young.		
	Agouti.	Black-red.	Albino.
Agouti ♂ 1509 × Agouti ♀ 1508.....	3	2	3
Agouti ♂ 1509 × Agouti ♀ 1507.....	2	0	0
Agouti ♂ 1509 × Agouti > red ♀ 1510..	2	1	0
Total.....	7	3	3

Other matings of agouti ♂ 1509 support the hypothesis that agouti gametes dominate over black-red ones. Thus he was mated with three different albino females derived from the same black-red-white spotted stock as his mother. The gametes of these females undoubtedly transmitted the black-red, never the agouti character. On the hypothesis that agouti is dominant over black-red, the young produced by these matings should be in the proportions, 2 agouti to 2 black-red to 4 albino ;

on the hypothesis of alternative dominance between agouti and black-red, the young should be in the proportions, 1 agouti to 3 black-red to 4 albino. The numbers observed are 2 agouti to 3 black-red to 5 albino—too few to be conclusive, but favoring the former hypothesis. On the whole it seems highly probable that agouti as a rule dominates over all other pigment combinations, but in the case of exceptional animals like ♀ 2020, page 27, black or black-red gametes may be formed which have a potency equal to that of agouti. This is an indication of individual prepotency like that discussed further on, under the heading, "Prepotency and Dominance."

*Agouti synthetically produced.*—An occasional animal with an excellent agouti coat may result from mating a red with a black individual. One such animal, ♂ 1178, tested as to the character of its gametes, apparently forms pure red and pure black gametes in approximately equal numbers, for mated with red females he has produced 3 red, 2 black, and 1 agouti young. His red gametes uniting with those furnished by the red females should produce red offspring, while his black gametes forming similar unions should produce either black or agouti young. Hence the result observed is exactly what we should expect, on the hypothesis that black and red have formed merely a temporary, not a permanent union in the agouti parent, and that the gametes formed by it contain either red or black, but not the two united in the agouti combination. What conditions, if any, can bring about a permanent union between segregated red and black my experiments do not as yet indicate.

#### THE BLACK TYPE.

My original black animals were obtained from Miss Soule. Bred *inter se* they produce only black offspring, though a few red hairs may usually be found by careful search somewhere on the body. The relation of black to agouti has already been discussed, so that we may pass immediately to its relations with red and with albinism.

*Black × red.*—The young produced by this cross have ordinarily a black coat, but of a reddish shade, as if the pigmentation of the black parent had been diluted with that of the red one; in other words, the characters of both parents show their influence in the offspring, which are not intermediate, only because black pigment is so much more opaque than red that the latter is scarcely visible. In other cases the weakening of the black pigmentation is seen in a restriction of the black pigmented areas, which then fall into the series of pigmented patches described on page 9, while red, or red and white together, fill up the intervening spaces. This results in the production of a black-red or black-red-white spotted animal. Or, thirdly, and less often still, the black and red may have the characteristic distribution which produces the agouti coat.

In detail, the matings which I have made under this category and their results are as follows :

Parents.	Young.		
	Reddish black.	Black > red.	Agouti.
♂ 2053 (black, but with a few red hairs) × red ♀ 755 .....	...	4	...
♂ 2053 × red ♀ 2031 .....	...	2	...
♀ 2013 (very deep black, without red hairs) × red ♂ 2054 .....	2	...	1
Total .....	2	6	1

Hybrids of all three sorts show segregation in forming gametes, though as yet not exactly in the expected Mendelian proportions. Thus the two reddish-black young of ♀ 2013 by ♂ 2054, viz, ♀ 1179 and ♂ 1180, have given the following results when mated with red animals :

Parents.	Young.				
	Red.	Yellow.	Black-red.	Black-yellow.	Agouti.
Black ♀ 1179 × red ♂ 2054 (father of ♀ 1179) .....	2	...	1	...	2
Black ♀ 1179 × red ♂ 2004 .....	2	...	2	...	...
Black ♂ 1180 × red ♀ 1073 .....	3	...	4	...	...
Black ♂ 1180 × red ♀ 1278 .....	3	...	1	...	...
Black ♂ 1180 × red ♀ 1279 .....	1	2	...	1	...
Black ♂ 1180 × red ♀ 1286 .....	2	...	...	...	...
Black ♂ 1180 × red ♀ 1307 .....	4	...	...	...	...
Black ♂ 1180 × red ♀ 2026 .....	2	1	1	...	...
Black ♂ 1180 × red ♀ 2027 .....	5	1	...	...	...
Total .....	24	4	9	1	2
	28		12		

It will be observed that ♀ 1179 has given by two different red males as close an approximation as is possible to the expected equality of red young on one hand and of black or agouti young on the other hand. But her brother, ♂ 1180, has produced a most astonishing excess of red individuals, more than three times as many red young being recorded as black ones. It would seem to be a peculiarity of this animal to form red gametes either more numerous or more vigorous than his black ones, for red young are in excess in all his matings

except one, that with ♀ 1073. Another unexpected result is the production of *weakly* pigmented animals of the red type, *i. e.*, of yellows, and of one yellowish-black (or blue) individual, where we expect only red and reddish-black offspring. The first mentioned peculiarity of ♂ 1180 is possibly shared by other cross-breds between the black and red types. Thus black > red ♀ 1156, a daughter of black ♂ 2053 by red ♀ 755, gave the following result:

Parents.	Young.	
	Red.	Agouti.
♀ 1156 × red ♂ 2054.....	1	1
♀ 1156 × red ♂ 2004 .. .. .	4	0

Again, reddish-black ♀ 3017, a daughter of the similarly pigmented ♀ 1179 by red ♂ 2054, gave by red ♂ 2004, three young, all red. The results thus far obtained by mating with red females the agouti ♂ 1178 (produced by the cross of black with red) have been previously given. They indicate that this hybrid forms red and black gametes in numbers approximately equal. Combining the results of all the matings made between an animal whose parents were red and black respectively, and red animals, we get 37 red (or yellow) to 14 black, blue, or agouti, where we should expect an equal number in each of the two general classes. Further experiments are needed to show whether the inequality thus far observed is a chance result which will disappear with larger numbers, or whether it is significant and will remain.

Several other black-red animals, which evidently contain recessive red, have produced, when mated with red animals, 8 black-red and 13 red young. The matings making up this total are as follows:

Parents.		Young.	
Black-red.	Red.	Black-red.	Red.
♂ 23.....	♀ 3.....	0	2
♂ 23.....	♀ 4.....	1	3
♂ 1227.....	♀ 1140.....	0	1
♂ 1288.....	♀ 1140.....	0	2
♂ 1448.....	♀ 1140.....	4	1
♂ 1482.....	♀ 1140.....	1	1
♂ 1607.....	♀ 1140.....	1	1
♂ 1165.....	♀ 1262 .. .	1	2
Total....	.....	8	13



Again, black-red pigmented animals which contain recessive red (or else latent red, see p. 25) when mated *inter se* have produced young as follows :

Parents.	Young.		
	Black-red.	Red.	Albino.
Black-red ♂ 23 × black-red (albino) ♀ 1 A.....	7	4	...
Black-red (albino) ♂ 89.1 <sup>a</sup> × black-red (albino) ♀ 1 A.....	...	2	...
Black-red ♂ 23 × black-red-white ♀ 51.2 <sup>b</sup> .....	3	4	...
Black-red (albino) ♂ 89.1 <sup>a</sup> × black-red-white ♀ 51.2 <sup>b</sup> .....	4	...	...
Black-red (albino) ♂ 89.1 <sup>a</sup> × black-red (albino) ♀ 89.3 <sup>b</sup> .....	1	...	1
Black-red ♂ 23 × black-red (albino) ♀ 89.3 <sup>b</sup> .....	6	...	...
Black-red ♂ 23 × black-red-white ♀ 209.....	1	1	...
Total.....	22	11	1

We should expect the black-red young to be three times as numerous as the red ones, but we find them only twice as numerous, yet the numbers involved are small, and the precise proportion observed probably not significant. Combining the results of all matings of black pigmented animals which are expected to produce red young we get a total of 105 young :\*

	Black pigmented.	Red pigmented.
Observed.....	44	61
Expected.....	61	44

*Black × albino.*—As elsewhere stated, few, if any, of my black animals are entirely free from red pigmentation, and my albinos, so far as determined, always possess latent red. Accordingly, more often than otherwise, the young produced by this cross show more or less red pigmentation, though in my experiments it has never amounted to more than a few red hairs, or one or two small red spots situated at the border of one of the typical pigment patches. The blackest young produced in this series of experiments resulted from matings between a very heavily black pigmented female (♀ 2012) and an albino male (♂ 635) part of whose gametes, as stated on page 24, entirely lacked the black character.

\* Further experiments made since the foregoing was written continue to give a steady excess of red animals and a corresponding deficiency of black ones.

In detail, the matings made are as follows :

Mating.	Parents.	Young.		
		Black.	Black > red.	Black > white.
(1)	Black ♀ 2012 × albino ♂ 635.....	7	1	1
(2)	Black ♀ 2012 × albino ♂ 2002....	...	2	2
(3)	Black ♀ 2014 × albino ♂ 2039....	...	3	...
(4)	Black ♀ 2014 × albino ♂ 2059....	...	3	...
(5)	Black > red ♂ 2053 × albino ♀ 807	...	4	...
(6)	Black > red ♂ 2053 × albino ♀ 766	...	5	...
	Total .....	7	18	3

The relation existing between the characters combined in this cross is one of simple Mendelian dominance, followed by segregation in the next generation, as is clear from the following matings :

Mating.	Parents.	Young.			
		Black.	Black > red.	Black > white.	Albino.
(7)	Black > white ♂ 1111 [born of mating (2) above] × albino ♀ .....	...	4	4	9
(8)	Black > red ♂ 1256 [born of mating (6) above] × albino ♀ .....	...	3	1	4
(9)	Black ♂ 1570 [born of mating (1) above] × albino ♀ .....	6	2	...	6
	Total .....	6	9	5	19
		20			

The hybrid males, it is evident, form in approximately equal numbers albino gametes and those bearing the centripetal type of pigmentation, and the latter transmit essentially the same kind of pigmentation as was possessed by the pigmented parent and the pigmented grand-parent. This conclusion is further supported by the result of matings of hybrids *inter se*, as shown on the following page.

Parents.	Young.			
	Black.	Black > red.	Black > white.	Albino.
Black > red ♂ 1256 [mating (6)] × black > red ♀ 1194 [mating (5)].....	3	...	...	...
Black > red ♂ 1256 [mating (6)] × black > red ♀ 1196 [mating (5)].....	1	3	...	2
Black > red ♂ 1256 [mating (6)] × black > red ♀ 1255 [mating (6)].....	2	...	...	1
Black ♂ 1570 [mating (1)] × black > red ♀ 1194 [mating (5)].....	...	2	...	1
Black ♂ 1570 [mating (1)] × black > red ♀ 1197 [mating (5)].....	...	2	...	1
Black ♂ 1570 [mating (1)] × black > white ♀ 3024 [mating (7)].....	...	1	2	1
Black ♂ 1570 [mating (1)] × black > white ♀ 3136 [mating (7)].....	...	1	1	...
Total .....	6	9	3	6
	18			

The result observed is in exact agreement with the expected Mendelian ratio, 3 : 1.

From what was said on page 24 concerning the transmission of pigment characters by albino gametes, we should expect that the character of the albino used in a cross with black would in some measure influence the result of the cross. That this is actually so is indicated by comparing results of matings (1) and (2), page 35, the black parent being the same in both matings, but the albinos markedly different. One of the albino males (♂ 635) forms gametes about half of which are entirely free from black; the other (♂ 2002) always transmits black pigmentation, frequently with a tendency to spotting. By the former were produced nine young, all but two of which were self-colored black; by the latter were produced four young, all spotted with red or black.

#### THE RED TYPE.

Red (including its dilute forms known as yellow and cream) is the only one of the three pigments of the coat which I have been able to obtain unquestionably free from the other two. Red and yellow animals not only form no black pigment in their hair, but appear to be incapable of transmitting the capacity to form black coat pigment. Red animals mated *inter se* ordinarily produce only red offspring, but reds obtained by cross-breeding with black may produce yellows when bred *inter se*. This case will receive further attention presently. Yellow mated with yellow produces, in my experience, only yellow offspring.

The relations of red to agouti and to black have already been discussed, and in part also that of red to albinism. Accordingly it remains only to consider in greater detail the last-named topic.

*Red* × *albino*.—The result of this cross depends upon what latent pigment characters are borne by the albino, and this in turn may in some cases be inferred from the ancestry of the albino, though in other cases not. Most of the albinos with which I have experimented contain latent black as well as red, and when mated with red or yellow animals produce invariably black-pigmented offspring. The matings indicated in Table D fall into this category of cases.

TABLE D.—*Matings of albinos (all of whose gametes transmit latent black) with red or yellow animals. The pigmented offspring all have black pigment in their coats.*

Parents.		Young.			
Albino.	Pure red or yellow.	Black-red.	Black-yellow.	Gold agouti-red.	Silver agouti-yellow.
Albino ♀ 644...	Red ♂ 2004.....	4	...	...	...
Albino ♀ 761.....	Red ♂ 2004.....	2	...	...	...
Albino ♀ 778.....	Red ♂ 2004.....	3	...	...	...
Albino ♀ 778...	Red ♂ 2054.....	...	1	2	...
Albino ♀ 779.....	Red ♂ 2004.....	4	...	...	...
Albino ♀ 1216...	Red ♂ 2054.....	2	...	1	1
Albino ♀ 1649...	Yellow ♂ 1347...	...	4	...	...
Albino ♂ 2002	Red ♀ 755.....	3	...	...	...
Albino ♂ 2002...	Red ♀ 784.....	2	...	...	...
Albino ♂ 2002...	Yellow ♀ 2001...	...	3	...	...
Albino ♂ 2039...	Red ♀ 753.....	4	...	...	...
Albino ♂ 2039...	Red ♀ 830.....	4	...	...	...
Total.....	.....	28	8	3	1

Albino.	Hybrid red or cream (albinism recessive).	Black-red.	Black-yellow.	Gold agouti-red.	Silver agouti-yellow.	Albino.
Albino ♀ "Himalayan."	Cream ♂ 1147....	...	3	...	...	4
Albino ♀ 766....	Cream ♂ 1147....	...	1	...	...	1
Albino ♀ 1027...	Red ♂ 1019.....	2	...	...	...	1
Albino ♀ 1028...	Red ♂ 1019.....	...	...	2	...	4
Albino ♀ 1544...	Red ♂ 1433.....	2	...	...	...	...
Albino ♂ 2002...	Red ♀ 683.....	2	...	...	...	...
Albino ♂ 2039...	Red ♀ 1020.....	1	...	...	...	2
Albino ♂ 2060...	Red ♀ 1355.....	...	...	1	...	1
Albino ♂ 2060...	Red ♀ 1442.....	...	...	2	...	2
Albino ♂ 2060...	Red ♀ 1476.....	3	...	...	...	4
Total.....	.....	10	4	5	...	19

Sixteen different albinos mated, as indicated in the table, with red, yellow, or cream animals, produced 59 pigmented young, all bearing black pigment.

Seven of my albino animals contain latent black, but transmit it apparently to only about half of their offspring. Matings of such albinos with red or yellow animals are enumerated in Table E.

The pigmented young produced by these matings are 41 black pigmented, 37 free from black pigment (*i. e.*, bearing only red or yellow pigment in their coats). The obvious explanation is that only *one* of the two gametes which united to form each of these albino parents contained latent black, the other being free from it; consequently only half the gametes formed by the albinos contain latent black.

TABLE E.—*Matings of albinos (part only of whose gametes transmit latent black) with red or yellow animals. Approximately half of the pigmented offspring have black pigment in their coats.*

Parents an albino and a pure red, red-white, or yellow animal.	Young.				
	Black-red.	Black-yellow.	Red.	Yellow.	Albino.
Albino ♂ 635 × red-white ♀ 43...	3	...	1	...	...
Albino ♂ 635 × red ♀ 470.....	2	...	...	...	...
Albino ♂ 635 × red ♀ 575.....	...	...	4	...	...
Albino ♂ 635 × red ♀ 610.....	2	...	...	...	...
Albino ♂ 635 × red ♀ 610 and red ♀ 753.....	5	...	3	...	...
Albino ♂ 635 × red ♀ 755.....	...	...	1	...	...
Albino ♂ 635 × red ♀ 830.....	2	2	4	1	...
Albino ♂ 635 × red ♀ 1073. ..	...	...	1	...	...
Albino ♂ 635 × red-white ♀ 1093.	5	...	1	...	..
Albino ♂ 635 × red ♀ 2008.....	...	...	3	...	...
Albino ♂ 635 × yellow ♀ 2001...	...	2	...	1	...
Albino ♀ 815 × yellow ♂ 2061..	..	1	...	3	...
Albino ♀ 1222 × red ♂ 2004.....	1	...	2	...	...
Albino ♀ 1222 × red ♂ 2054.....	1 (agouti-red.)	...	1	1	...
Albino ♀ 1224 × yellow ♂ 1347....	...	1	...	2	...
Albino ♂ 1516 × red-white ♀ 1387 .....	3	...	1	...	...
<b>Total.....</b>	<b>24</b>	<b>6</b>	<b>22</b>	<b>8</b>	<b>...</b>
	30		30		

Parents an albino and a red, red-white, or yellow animal with recessive albinism.	Young.				
	Black-red.	Black-yellow.	Red.	Yellow.	Albino.
Albino ♂ 635 × red-white ♀ 690..	1	...	1	...	1
Albino ♂ 1516 × red-white ♀ 1344.	2	...	...	...	2
Albino ♀ 1516 × yellow ♀ 1346...	...	2	...	...	1
Albino ♂ 1516 × yellow ♀ 1348....	...	2	...	...	...
Albino ♀ 1516 × red-white ♀ 1434.	1	...	1	...	2
Albino ♀ 1216 × red ♂ 1386.....	...	...	1	...	...
Albino ♀ 1224 × red ♂ 1386.....	1	...	3	...	...
Albino ♀ 1236 × red ♂ 1386.....	2	...	1	...	...
<b>Total.....</b>	<b>7</b>	<b>4</b>	<b>7</b>	<b>...</b>	<b>6</b>
	11		7		

A means of testing the validity of this explanation has been suggested by Allen (: 04) for the similar case of chocolate pigmentation in mice. If the albino gametes which contributed to the production of the red or yellow offspring in the matings last mentioned were really *free* from black, then two of these hybrid red animals (containing recessive albinism) when mated should produce albino offspring *not any* of whose gametes contain latent black. Experiment has shown this to be the actual result. Albino ♂ 1999 was produced by mating two hybrid yellow animals containing recessive albinism. He has been several times mated with yellow females (see Table F) and has produced 13 pigmented offspring, all yellow. As a control he was mated also with a black female containing recessive albinism. This mating produced 3 albinos and 1 *black* pigmented young. Another albino tested, ♂ 2059, is apparently similar in nature to ♂ 1999, for when mated with red ♀ 610, he produced 3 young, all red pigmented (see Table F). The ancestry of this albino is unknown to me, as I obtained him from a breeder, and as no other test of this sort was made in his case, the result can not be considered conclusive, because of the small number of young produced; but it is probable that all his gametes were free from latent black, for four of his albino daughters by albino mothers containing latent black form albino gametes free from black, as well as other gametes containing black. They are ♀♀ 1216, 1222, 1224, and 1236, Table E. Each of these four daughters of ♂ 2059, all that have been tested, must have received from the father albinism free from latent black, for the mothers, as stated, did not form gametes containing latent black.

TABLE F.—*Matings of albinos (not any of whose gametes transmit latent black) with red or yellow animals. Not any of the offspring are black pigmented.*

Parents.		Young.		
Albino.	Pure red or yellow.	Red.	Yellow.	Albino.
♂ 1999.....	Yellow ♀ 3105.....	...	3	...
♂ 1999.....	Yellow ♀ 3200.....	...	3	...
♂ 1999.....	Yellow ♀ 3085.....	...	5	...
♂ 2059.....	Red ♀ 610.....	3	...	...
Total.....	.....	3	11	...
Albino.	Yellow (albinism recessive).	Red.	Yellow.	Albino.
♂ 1999.....	♀ 1346.....	...	...	3
♂ 1999.....	♀ 1348.....	...	...	2
♂ 1999.....	♀ 2063 and 3036.	...	2	1
Total.....	.....	...	2	6

Although the discovery of the differences among albinos, as regards matings with red animals, was made by mere accident while comparing the matings of ♂ 635 with those of other albino males, I have since found it possible to produce at will albinos free from latent black (like ♂ 1999) by beginning with matings between ordinary albinos (all of whose gametes transmit latent black) and red or yellow animals. The following case illustrates the method used : Albino ♂ 2002 is shown by matings recorded in Table D to form only gametes transmitting latent black. For by red or yellow females he has produced 10 pigmented young, all with more or less black in their coats. From the mating with yellow ♀ 2001 there resulted 3 black-yellow young, ♀♀ 2033-2035. Each of these, according to the hypothesis offered, received from one parent albinism with latent black, and from the other yellow free from black. In forming gametes the yellow-black hybrids should produce gametes of four different kinds, all equally numerous (on the hypothesis that albinism is inherited independently of specific pigments,

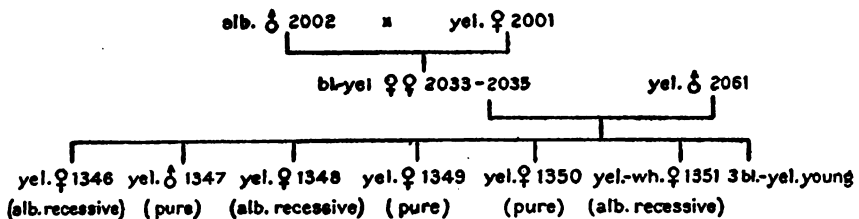


FIG. 10.—A genealogical table ; for description, see text.

as previously explained, viz, (1) yellow, (2) black, (3) albinism [yellow latent], (4) albinism [black latent]. Accordingly, when a mating of such a hybrid is made with a pure yellow animal, such as ♂ 2061 (see fig. 10), gametic unions of four different sorts should occur with equal frequency, viz, (1) yellow + yellow, producing pure yellow young ; (2) black + yellow, producing black-yellow young free from recessive albinism ; (3) albinism [yellow latent] + yellow, producing yellow young (with albinism recessive) ; (4) albinism [black latent] + yellow, producing black-yellow young (with albinism recessive). That is, half the young should be yellow, half should be black-yellow ; and of each sort half again should contain recessive albinism, half should be free from it. In the case under discussion (see diagram, fig. 10) there were produced 6 yellow and 3 black-yellow young, but in a series of matings equality of the two classes would undoubtedly have been more closely approximated, as Table E indicates. The yellow young alone were tested for the presence of recessive albinism, and it was found in exactly half of them, viz, ♀♀ 1346, 1348, and 1351, the test indicating that the other three yellow young are pure. The method by which

albinos free from latent black may be obtained from red or yellow hybrids, like ♀♀ 1346, 1348, and 1351, has already been explained. It is simply to mate the hybrids *inter se*, when there should be produced albino young, approximately one-fourth of all the young produced, and these albinos should be free from latent black. A number of albinos have been so produced in these experiments, but only one of them, viz, ♂ 1999, Table F, has yet been tested. It is evident that his gametes are, as expected, free from latent black.

This experiment indicates methods of practical utility to the breeder who desires either albinos as free as possible from peripheral pigment

TABLE G.—*Matings inter se of red or yellow animals having albinism recessive. None of the young black-pigmented. Expected proportion of albinos 1 in 4.*

Parents.	Young.		
	Red or red-white.	Yellow or yellow-white.	Albino.
Red ♂ 1019 × red ♀ 4.....	7	...	1
Yellow ♂ 1147 × yellow ♀ 1032.....	...	3	...
Yellow ♂ 1147 × yellow ♀ 1487.....	...	3	2
Yellow ♂ 1147 × yellow ♀ 1489.....	...	3	1
Yellow ♂ 1147 × yellow ♀ 1786.....	...	...	2
Yellow ♂ 1147 × red ♀ 2029.....	2	1	...
Red ♂ 1433 × red ♀ 1643.....	3	...	...
Red ♂ 1453 × red ♀ 1291.....	2	2	...
Red ♂ 1453 × red ♀ 1292.....	3	...	...
Red ♂ 1453 × red ♀ 1297.....	2	1	...
Red ♂ 1453 × red ♀ 1299.....	2	...	...
Red ♂ 1453 × red ♀ —?.....	4	...	...
Red ♂ 1477 × red ♀ 1292.....	3	1	...
Yellow ♂ 1998 × yellow ♀♀ 1351 and 1535..	...	4	2
Total.....	28	18	8
	46		

or animals of various shades of red or yellow. For (1) albinos free from latent black have much less peripheral (chocolate or chocolate and black) skin pigment than others, and (2), when mated with red or yellow animals they frequently produce young of a *lighter* shade of red or yellow than that of the pigmented parent. He who mates ordinary albinos with red animals in hope of obtaining yellows will be sorely disappointed, for the young will be mottled with black (received latent from the albino parent); but he who employs albinos, such as I have described, in matings with red or yellow animals, may doubtless with patience realize his fondest hopes. By this method I have been able to produce cream-colored animals of a much lighter shade than any I ever saw before. Theoretically it should be possible by following up this method to produce animals practically white, but



with dark eyes. Time will show whether this is possible. It is not improbable that practical difficulties may be encountered. Experienced breeders say that the "purest" albino guinea-pigs (*i. e.*, those most free from peripheral pigmentation) incline to sterility. Two cases which have occurred in my own experiments make me think there is some truth in this idea. Further, albinos free from latent black have not yet been mated *inter se*, but I shall not be surprised

TABLE H.—*Matings of males mentioned in Table G with animals black pigmented, but having albinism recessive. The expected proportion of albinos is 1 in 4.*

Parents.	Young.				
	Black-red.	Black-yellow.	Yellow.	Agouti-yellow.	Albino.
Red ♂ 1019 × agouti ♀ 2020.....	2	...	..	...	...
Yellow ♂ 1147 × black-yellow ♀ 1149 .....	...	...	...	...	3
Yellow ♂ 1147 × silver agouti-yellow ♀ 1252.....	...	..	1	2	...
Yellow ♂ 1147 × black-yellow ♀ 2034.....	...	1	1	...	...
Total.....	2	1	2	2	3
	7				

TABLE I.—*Matings of males mentioned in Table G with albino females. It is expected that half the offspring will be albinos.*

Parents.	Young.			
	Black-red.	Black-yellow.	Agouti-red.	Albino.
Red ♂ 1019 × albino ♀ 1025.....	...	...	2	4
Red ♂ 1019 × albino ♀ 1027.....	2	...	...	1
Yellow ♂ 1147 × albino ♀ "Himalayan"	...	3	...	4
Yellow ♂ 1147 × albino ♀ 1194.....	...	...	...	2
Yellow ♂ 1147 × albino ♀ 815.....	...	...	...	2
Red ♂ 1433 × albino ♀ 1544.....	2	...	...	...
Total.....	4	3	2	13
	9			

to find them relatively unproductive when this is done, for the hybrids bred *inter se* have in certain cases produced fewer *albino* young than they should produce on the Mendelian hypothesis. Thus, an examination of Table G shows that only 8 albinos have been produced in a total of 54 young, where 13.5 are expected. Nevertheless, this may be only a chance deviation from the expected proportion of albinos which will disappear as larger numbers are produced. Tables H and I indicate that the hybrid males employed in the matings enumerated

in Table G really produce a full quota of albino gametes, and that these are entirely fertile when they meet gametes transmitting black, either active or latent.\*

It is a question of much interest, theoretical as well as practical, whether animals of a particular type, when produced by cross-breeding, form the same sort of gametes as are produced by pure-bred animals of the same type. In the case of albinos this evidently is not always true. From an albino which forms gametes all of which transmit latent black, there may be produced, as we have seen, by cross-breeding with a red animal and then interbreeding the hybrids, albinos of three different sorts as regards the transmission of latent black pigment. Again, the character of a red race which breeds true may be modified by cross-breeding with black, resulting in the production of yellow young. Thus two red animals, young of black (red recessive)

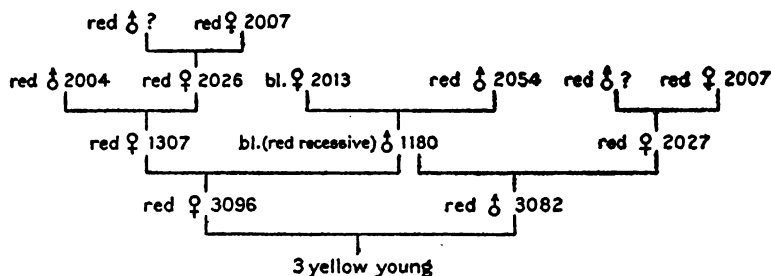


FIG. 11.—A genealogical table showing how cross-breeding between red and black may cause variation in the intensity of the red.

♂ 1180, by two different pure-bred red females, when mated together, produced a litter of 3 yellow young. The relationships involved will perhaps be more readily understood from the above diagram (fig. 11).

Apparently the cross with black induced variation in the intensity of the pigmentation transmitted by the gametes bearing red, so that some of the zygotes which were formed bore the dilute form of red, viz, yellow.

#### BLACK-EYED WHITE.

Guinea-pigs of this sort have hair and skin very free from pigment, indeed in the integument of the living animal I can detect no pigment at all, yet the eyes are black pigmented. Two animals of this sort have been born in the course of my experiments, and I have likewise experimented with two others obtained by purchase. They are not albinos and do not contain recessive albinism, at least those which I have had do not. They are of spotted parentage and may be considered spotted animals in which the typical pigment patches show an extreme

\*Experiments made since the foregoing was written show that albinos free from latent black are entirely fertile *inter se*. Further, the deficiency of albinos observed at first is now disappearing.

condition of reduction. The successive steps by which the pigmentation of guinea-pigs undergoes reduction are about as follows: (1) The pigment centers are all functional, but the pigment areas do not quite meet along the middle of the ventral surface, or in the forehead. Perhaps the pigment fails to reach one or more of the feet also. (2) One or both shoulder patches are wanting, producing the Dutch-marked type (compare fig. 6, p. 12). (3) The side patches are also wanting; only the rump and sides of the head are pigmented (fig. 2, p. 10). (4) The rump patch disappears; only the sides of the head are pigmented, and here the patches are small, or one or more of them may be wanting (fig. 4, p. 11). An extreme condition of this sort is represented by ♂ 721, whose coat was entirely unpigmented except for a small patch of black about 5 mm. square on the outer surface of his right ear. (5) The skin is wholly unpigmented, though the eyes are as in all the foregoing stages dark. One can by selection progress in either direction through this series of changes, either increasing or decreasing the number and extent of the pigment patches, but it is impossible without long-continued selection to fix the color pattern at any particular stage in the series; perhaps it is wholly impossible to do so, as Cuénot (:04, p. LV) asserts on the basis of his studies on mice, but this I very much doubt. I doubt it first, because we do find color patterns of this sort firmly fixed in many wild species, such as antelopes, skunks, etc.; secondly, and still more, I doubt it because of what we see accomplished in domesticated animals. Take the case of cattle alone. Different breeds of cattle have often distinctive color patterns, as well as specific pigments in their coats. Holstein cattle are white, marked with large but more or less irregular black spots, the color pattern being apparently not definitely fixed. Dutch belted cattle, probably derived from the same general source as the Holstein, have for a long time been subjected to a rigid selection for a more definite color pattern, viz, an animal wholly black except for a broad white belt around the middle of the body. To this type the breed is said to keep very true.

Pure-bred Hereford cattle as kept at the present time in America are red over the greater part of the body, but are invariably white-faced; a longitudinal white stripe extends down the middle of the back, and the belly and flanks are more or less extensively marked with white. The white face, though now rigidly insisted upon and always seen in pure-bred herds, has not always been so common in the breed. A half century or more ago, according to Shaw (:03), rival breeders advocated white-faced and mottled-faced Herefords, but the former prevailed, and by continued selection the mottled-faced condition has now apparently been eliminated from the breed.

These cases indicate that certain of the typical color patches, as, for example, the cheek patches of cattle, can by continued selection be

eliminated altogether, while others are kept at their maximum intensity. How this is possible we could understand better if we knew in what condition pigment characters are transmitted in the germ. From the experimental evidence alone it would seem probable that the different color patches are represented in the germ by different elements separately heritable, possibly in different chromosomes—though of this we know absolutely nothing—and that as a result of long selection these separately heritable elements may become firmly associated with particular body regions. From the mode of development of the hair pigments as described by Leo Loeb ('97) and confirmed by observations of Mr. Howard and myself, it is clear that the pigments are formed in the Malpighian layer of the epidermis. A pigment patch, then, is, morphologically, simply the pigmented epidermis of a particular body region, and its character is determined by whatever determines the character of the epidermis in that body region.

That black-eyed white animals are essentially animals of the centripetally pigmented type is shown by breeding them *inter se* or by mating them with albinos. In every case thus far I have obtained only young with one to several, or even with *all*, of the typical pigment patches. The task of establishing a black-eyed white race which will breed true is similar to that of establishing a Dutch-marked race which will breed true, or in cattle a white-faced race like the Hereford. It is not to be accomplished in a single generation, but I doubt not its possibility. When guinea-pigs have been bred to a particular color pattern for many generations, we can form a better estimate of the magnitude of the task involved, and possibly meantime may learn something about the mechanism of transmission of the color patches.

The specific pigments transmitted by black-eyed white animals are probably determined by the same rules that govern in the latent pigmentation of albinos. These pigments probably differ according to the parentage in different cases, or more correctly according to the latent pigmentation which each individual received from its parents. Indeed, it is not impossible that vanished pigment patches are merely *latent* pigment patches, and that the reason why these keep reappearing in such a seemingly erratic fashion is that they keep emerging from latency under the influence of cross-breeding. In the black-eyed white animals with which I have experimented, red as well as black spots are apparently transmitted in the gametes formed, but I should expect that in animals different in origin red might be transmitted apart from black or *vice versa*.

I have not examined with the microscope the eye-pigments of the different self-colored varieties of the guinea-pig. From a superficial examination, however, I should say that black pigment is present in

every case except that of the albino. Yet we have seen that red and yellow animals, which have no black pigment in their coats, do not transmit black coat-pigment to their offspring, though they do transmit black eye-pigment. We might conclude that eye-pigment is something altogether different from and independent of coat-pigment, but two considerations negative this idea : (1) Black-eyed white animals mated with albinos produce animals with coat-pigment in the typical patches, a thing which neither parent possessed ; (2) in mice, animals with coat patches but devoid of eye-pigment, when mated with unrelated albinos, produce offspring with pigmented eyes, again a character which neither parent possessed (Darbishire, :04). From these facts we see that a certain connection does exist between eye-pigmentation and coat-pigmentation, though apparently it is less close than that between one coat-patch and another coat-patch. The disappearance of eye-pigmentation, like the disappearance of coat-pigmentation, is probably due, in the case of ordinary albinos, to *latency* in the germ of a particular hereditary unit. This condition of latency, it is evident, can be made to disappear by cross-breeding with any animal of the centripetally pigmented type. But in centripetally pigmented animals, as we shall see, disappearance of eye-pigment, when once it has occurred, is apparently beyond recall, at least by cross-breeding with albinos. This is indicated by the instructive experiments of Darbishire ( : 04), which we shall presently examine more in detail.

A condition which might be described as semi-latency of a coat-pigment was observed in the case of a red-white animal, ♀ 915, which was mated with red ♂ 1019. To my great surprise she produced in two successive litters four young having *black-red* coats. This was contrary to any previous experience (compare Table G), and I at once sought for an explanation. Upon looking the animal over carefully I found, what I had before overlooked, that she had a sacral patch of *black skin*, though not a single hair of her body, so far as I could discover, was black pigmented. The capacity to form black integumentary pigment was evidently present in the animal, though its influence extended only to the epidermis proper, not to the hair-follicles. One often sees in dogs, for example in fox-terriers, black skin spots of this sort in body regions where the coat is entirely white. The character semi-latent in ♀ 915 came into full activity in four of her offspring by a male devoid of that character.

Black skin is not infrequently seen on the feet of red guinea-pigs, but such animals do not produce young with black hairs when they are mated with other red animals. A comparison of this result with that described in the case of ♀ 915 serves to emphasize the distinction which has been made between centrifugal and centripetal pigmentation

(see p. 9). The black-footed guinea-pig has the former, which it transmits to its offspring; it does not possess the latter and its offspring never do, unless a mating has been made with an animal having pigmentation of that sort. The black-footed red guinea-pig, as regards black pigmentation, is in exactly the same condition as an albino with dark-pigmented extremities; centripetal black pigmentation is fully latent in it.

Black-eyed white animals, of the sort which I have had, and animals like ♀ 915, are centripetally pigmented animals in which the capacity to form black pigment in the typical central patches is *semi-latent*, *i. e.*, they may apparently transmit the character in a fully active condition, when mated *inter se*, a cross with animals having a different type of pigmentation being unnecessary for this purpose.

Darbshire's pink-eyed but centripetally pigmented mice, if they possessed at all the capacity to form eye-pigment, must have possessed it in a more than latent condition, for they bred true *inter se*, and though a cross with albinos brought the character into full activity, there are strong reasons for believing, as we shall presently see, that the capacity to form eye-pigment was recovered, not from the pink-eyed animal, but from the albino with which it was mated. It is to be expected that continued selection and inbreeding of black-eyed white guinea-pigs would establish a condition of the coat-pigment patches similar to that of the character eye-pigmentation in Darbshire's pink-eyed mice, a condition which goes beyond the latency of centripetal pigmentation in albinos, and may, for all we at present know, amount to elimination of the character in question from the germ. This question offers an attractive field for further investigation.

*Comparison with pink-eyed mice.*—The dark-eyed mice obtained by Darbshire (: 04) upon mating pink-eyed spotted mice with albinos, yielded an interesting result when bred *inter se*. Approximately one-fourth of the young were, as we should expect, albinos; one-half were dark-eyed, like their parents, the primary hybrids; and one-fourth were pink-eyed and spotted. We should naturally expect the dark-eyed young (like their parents) to contain recessive albinism, and the pink-eyed spotted ones to be free from it, like their pink-eyed grandparents. While in many cases this was undoubtedly true, in others it was not true; for Darbshire's breeding experiments show that some of the dark-eyed animals did not contain recessive albinism, and that some of the pink-eyed ones did. Further, the "extracted" albino young in some cases behaved differently from their albino grandparents in crosses with pink-eyed spotted animals. They produced pink-eyed as well as dark-eyed hybrids, the two sorts being approximately equal in number (7 pink-eyed to 6 dark-eyed, Darbshire, : 04, Table D, p. 24).

From this it is clear that the five albino parents which gave the result just described transmitted in approximately half their gametes the pink-eyed and in half the dark-eyed condition. These albinos are comparable in the matter of the pink-eyed character with my albino guinea-pigs of Table E in the matter of black coat-pigment. A close parallel exists throughout the two cases. Darbishire's original albinos all contained latent the character pigmented eye. This character was invariably brought into activity by a cross with the centripetally pigmented but pink-eyed race. That race would seem not to have possessed the character eye-pigmentation, even in a state of latency which a cross with albinos would bring into activity; for half the gametes formed by the hybrids apparently lacked the character eye-pigmentation, and that character was as often associated latent with the albino character, as it was associated active with the alternative character, standing for centripetal pigmentation. If so, the hybrids must have formed with equal frequency gametes of these four sorts: (1) pigmented coat, pink-eye,\* (2) pigmented coat, dark-eye, (3) albinism [pigmented coat and pink-eye latent], (4) albinism [pigmented coat and dark-eye latent].

Hybrids forming sets of gametes like these, when mated *inter se*, should produce young visibly of three classes in the proportions, 9 dark-eyed pigmented to 3 pink-eyed pigmented to 4 albino. The numbers observed by Darbishire are 287 (or 284?) dark-eyed pigmented, 131 (or 134?) pink-eyed pigmented, and 137 albino young.

On the hypothesis which I have suggested, these young, though visibly of only three different sorts, should really fall into nine classes, whose numerical proportions are theoretically as follows:†

Class (1), 4 $Pd(Ap)$	} 9 pigmented dark-eyed.	Class (5), 2 $Pp(Ap)$	} 3 pigmented pink-eyed.
Class (2), 2 $Pd(p)$		Class (6), 1 $Pp$	
Class (3), 2 $Pd(Ad)$		Class (7), 2 $A[d p]$	} 4 albinos.
Class (4), 1 $Pd$		Class (8), 1 $A[d d]$	
		Class (9), 1 $A[p p]$	

This classification rests on the assumption that eye-pigmentation may be inherited apart from coat-pigmentation, *i. e.*, that the primary hybrids are really *di*-hybrids in the Mendelian sense. It involves the further hypothesis that eye-pigmentation was invariably latent in the original albino stock used, and as invariably absent from the pink-eyed

\* Although the pink eye is due merely to *absence* of pigment from the eye, just as albinism to absence of pigment from the eye and coat, it is convenient in both cases to speak of the negative character as if it were positive. This can be done, I trust, without confusion to the reader.

† EXPLANATION.— $A$  = albino;  $P$  = pigmented;  $d$  = dark-eyed;  $p$  = pink-eyed; ( ) indicate recessive characters, [ ] latent characters. The relative frequency of occurrence of individuals of each class is indicated by a coefficient.

pigmented animals (at least in a state capable of becoming active as a result of matings with albinos).

Let us now inquire whether Darbishire's experiments indicate the existence of these various hypothetical classes or not. Darbishire gives in the first part of his Table E, page 35, the results of mating *inter se* dark-eyed pigmented animals of generation  $F_1$ .<sup>\*</sup> On the "ancestry" hypothesis these should all breed much alike, for their ancestry is similar in all cases; on the hypothesis which I have stated, they include the four distinct sorts of individuals which I have called classes (1) to (4), page 48, and these will breed very differently one from another. An examination of Darbishire's table shows that in fact the various pairs of pigmented dark-eyed animals gave results of four different sorts.

I. The following pairs gave young of three sorts—dark-eyed, pink-eyed, and albino :

Pair.	Young.		
	<i>P d.</i>	<i>P p.</i>	<i>A.</i>
2H 48.....	2	1	2
2H 52.....	3	1	1
2H 93.....	2	2	1
Total. ....	7	4	4

On the Mendelian hypothesis each of the parents in these three families must have furnished gametes bearing the pink-eyed character as well as gametes bearing the albino character. If so, and if each of these characters was represented in *half* the gametes formed, and the two characters were independent of each other, then the parents were of class (1), page 48, and the young should be as 9 *P d* to 3 *P p* to 4 *A*, which approximates roughly the observed 7 to 4 to 4.

II. The following pairs gave only dark-eyed and pink-eyed young, without albinos :

Pair.	Young.	
	<i>P d.</i>	<i>P p.</i>
2H 39 $\alpha$ .....	5	2
2H 39 $\beta$ .....	4	1
2H 53 $\beta$ .....	4	1
2H 139.....	4	1
2H 142... ..	6	2
Total... ..	23	7

<sup>\*</sup>I adopt here and in the following pages Bateson's convenient notation for the successive "filial" generations following a cross, viz,  $F_1$ ,  $F_2$ ,  $F_3$ , etc.



A result of this sort can have followed either from matings *inter se* of animals of class (2), page 48, or from matings of such animals with those of class (1). In either case the young should be as 3 *Pd* to 1 *Pp*, a ratio closely approximated in the observed 23 *Pd* to 7 *Pp*.

III. The following pairs gave only dark-eyed and albino young, without pink-eyed pigmented ones :

Pair.	Young.	
	<i>Pd.</i>	<i>A.</i>
2H 50 $\alpha$ .....	4	1
2H 50 $\beta$ .....	4	1
2H 53 $\alpha$ .....	7	1
2H 96.....	6	1
2H 99.....	3	2
Total.....	24	6

Such a result would be produced either by mating *inter se* individuals of class (3), page 48, or by mating individuals of that class with those of class (1). In either case the young should be as 3 *Pd* to 1 *A*. The observed numbers, 24 to 6, are not greatly at variance with this ratio, considering the small number of young produced.

IV. The following pairs produced only dark-eyed pigmented young, without either albinos or pink-eyed pigmented young ;

Pair.	Young.
	<i>Pd.</i>
2H 36.....	3
2H 49.....	6
2H 51.....	5
2H 92.....	3
Total.....	17

Such a result should follow mating *inter se* two individuals of class (4), page 48, or mating an individual of that class with one from any of the other three classes, (1) to (3), or from a mating between classes (2) and (3).

Accordingly, in the eighteen pairs which Darbishire formed of dark-eyed pigmented mice of this second filial generation (omitting only one pair which gave but a single young), we get evidence of the probable existence of all four of the hypothetical classes of dark-eyed individuals. If the pairs were taken quite at random without regard to the recessive characters present in the different animals (and this was evidently the case, since Darbishire does not admit the existence

of such characters), we should expect from the theoretical numerical frequencies of classes (1) to (4) that pairs giving the four sorts of results described would be as follows. The observed frequencies are for convenience in comparison given in a parallel column.

Group.	Expected frequency.	Approximately.	Observed frequency.
I .....	28	3	3
II .....	38	4	5
III .....	38	4	5
IV .....	53	6	4

The agreement between expected and observed frequencies, it will be noticed, is as close as could reasonably be expected in so small a number of pairs.

Again, Darbishire mated dark-eyed animals, like those whose matings we have been discussing, with dark-eyed animals of different parentage, one of the parents having been a hybrid, the other an albino. In all such cases the albino parent evidently possessed and transmitted to its offspring the dark-eyed character, for none of the pigmented young were pink-eyed. But the hybrid parent, according to our hypothesis, transmitted the pink-eyed character to half its offspring, forming gametes as follows (see p. 48):  $Pd + Pp + A[d] + A[p]$ .

Union of the gametes of the albino parent, all  $A[d]$ , with gametes like these would produce young as follows:

$$Pd(Ad) + Pp(Ap) + A[dd] + A[dp].$$

But as Darbishire utilized in the experiment under discussion only pigmented animals, we are concerned at present only with the first two classes of young. They are identical in character with individuals of classes (3) and (1), respectively (p. 48), but occur in equal numbers, whereas in a group of hybrids like that described on page 48, class (1) is twice as abundant as class (3).

The question now before us is, if individuals of classes (1) and (3) be taken with equal frequency to mate with individuals taken at random from a mixture of classes (1) to (4) in the proportions indicated on page 48, what sorts of offspring are to be expected and in what proportions in the various pairs formed. Making the calculations by the methods already explained, we find that pairs should occur giving the same four sorts of results as in the previous case (pp. 49 and 50, I to IV); but these pairs should occur in frequencies somewhat different.

The pairs recorded by Darbishire (p. 35, Table E, middle section) which fall into these respective groups are as follows (omitting only one pair which produced 3 albinos and which might fall into either Group I or Group III) :

GROUP I.				GROUP II.		
Pair.	Young.			Pair.	Young.	
	<i>Pd.</i>	<i>Pp.</i>	<i>A.</i>		<i>Pd.</i>	<i>Pp.</i>
2H 23 .....	2	1	2	2H 28.....	4	1
2H 34.....	5	1	1	2H 33.....	5	1
2H 38.....	2	3	1	2H 43 .....	5	3
2H 44 <sup>a</sup> .....	5	1	1	2H 107.....	3	3
Total.....	14	6	5	Total .....	17	8
Expected.....	9	3	4	Expected.....	3	1

GROUP III.			GROUP IV.	
Pair.	Young.		Pair.	Young.
	<i>Pd.</i>	<i>A.</i>		<i>Pd.</i>
2H 29.....	3	1	2H 32.....	5
2H 41.....	4	1	2H 40.....	3
2H 44 <sup>b</sup> .....	3	2	2H 103.....	5
2H 101.....	5	2	2H 118.....	5
2H 106.....	2	2		
2H 119.....	4	2		
2H 145.....	3	2		
Total .....	24	12	Total .....	18
Expected.....	3	1	Expected.....	all <i>Pd.</i>

The expected relative frequencies of these four sorts of pairs are as follows, the frequencies observed being given in a parallel column :

Group.	Expected frequencies.	Observed frequencies.
I .....	4	4
II .....	2	4
III .....	8	7
IV .....	4	4

From this experiment we get additional evidence of the existence of the four hypothetical classes of dark-eyed pigmented individuals, (1) to (4), page 48, and of their occurrence in something like the theoretical proportions. Still further support for this view is afforded by the third section of Darbishire's Table E, page 35, which includes matings of

dark-eyed animals, each having one albino and one hybrid parent. Half of these animals should have the character of class (1), p. 48, and half that of class (3). Pairs established by random selection of individuals should, therefore, be in the proportions, 1 mating within class (1) to 2 matings between classes (1) and (3) to 1 mating within class (3). Pink-eyed pigmented young should be produced only in matings of the first sort, but albinos should result from all three sorts of matings.

The matings which produced pink-eyed young are as follows :

Pair.	Young.		
	<i>Pd.</i>	<i>Pp.</i>	<i>A.</i>
2H 18.....	2	2	2
2H 27.....	4	1	...
2H 111.....	3	1	...
2H 116.....	...	4	2
2H 143.....	5	2	...
2H 146.....	3	3	1
2H 147.....	3	1	4
2H 148.....	4	5	...
Total.....	24	19	9
Expected .....	9	3	4

The remaining matings are as follows :

Pair.	Young.	
	<i>Pd.</i>	<i>A.</i>
2H 19.....	4	1
2H 20.....	5	2
2H 22.....	4	1
2H 25.....	1	3
2H 26.....	4	2
2H 37.....	3	3
2H 45.....	3	3
2H 110.....	3	...
2H 112.....	8	...
2H 113.....	2	3
2H 114.....	4	...
2H 115.....	3	1
2H 144.....	4	2
Total.....	48	21
Expected.....	3	1

The evidence from the group of matings contained in these two lists is less clear than that from the two groups previously examined. There is a considerable excess of pink-eyed young in most of the mat-

ings which produced offspring of that character, and a deficiency, almost as great, of albinos. If these deviations from the expected proportions indicate anything other than a chance result, it is an increase in the proportion of gametes bearing the character pink-eye associated with pigmented coat, and a corresponding diminution in the proportion of albino gametes. Yet such a change is of very doubtful occurrence; more probably the outcome is a chance one, for the deficiency of albinos produced by the eight pairs which had pink-eyed young is more than offset by an excess of albinos produced by the other thirteen pairs, the total young produced being 121 pigmented to 30 albinos.

The fact, too, that certain pairs of this category produced *no* albinos must not be taken as conclusive evidence that the animals mated did not contain recessive albinism. The expectation is that only 1 in 4 of the young produced will be albinos, and it is not surprising that, as a chance result, *no* albinos should be found among as few as the 3 to 9 young produced by a pair. More extensive tests, or the simpler test of mating with albinos, would without doubt have shown the formation of albino gametes by each of the parents in question, if they really were of the parentage indicated in Darbishire's table.

The foregoing considerations indicate that the correctness of the classification of pairs in the cases previously examined is not established beyond question. For example, a pair which in a total of 6 or 8 young has produced only those of two sorts, might in subsequent litters produce young of the third sort, which would place the parents in a different category. Only in the cases where young of all three sorts have been produced is the character of a pair conclusively established. In other cases the probability of correctness in the classification made increases with the number of young produced. Whatever errors are involved tend to increase the magnitude of Group IV (pp. 50 and 52) at the expense of Groups I to III, and that of II and III at the expense of I. Making all allowance for such possible errors, there would still seem to be little reason to question the existence, among Darbishire's dark-eyed mice of generation  $F_2$ , of all the four classes designated (1) to (4) on page 48.

The existence of the two classes of pink-eyed pigmented mice (5) and (6), page 48, is strongly indicated by matings *inter se* of pink-eyed mice belonging to generation  $F_2$ , as recorded by Darbishire in his Table H, page 37. According to our hypothesis, the pink-eyed mice of this generation are in character either  $Pp$  or  $Pp (Ap)$ , individuals of the latter sort being twice as numerous as those of the former. Not any of them contain the dark-eyed character; consequently they should produce only pink-eyed young or albinos, when bred *inter se*. The

seven pairs tested by Darbishire produced 31 pink-eyed and 1 albino young, with no dark-eyed ones—conclusive evidence against the “ancestry” hypothesis of Galton and Darbishire, for all four grandparents were dark-eyed. The number of young produced by a pair in this experiment ranged from 2 to 6, the single albino occurring in a litter of 5. This one albino gives conclusive evidence that its parents both contained recessive albinism and so were of class (5). We should on the theory of probabilities expect the occurrence of *three* such pairs in seven taken at random. It is possible that more extensive tests would actually have shown the occurrence of more than this one, but it is a probability which amounts almost to a certainty that not *all* the seven pairs would have given albinos, had they been more extensively tested. If not, then the occurrence of individuals of class (6), *i. e.*,  $Pp$ , would be fully established by the experiment. But the absence of recessive albinism from certain of the pink-eyed mice of this generation is shown in a simpler way, viz, by matings with albinos. Nineteen such matings are recorded by Darbishire in his Table G, page 36. The number of young produced by a pair ranges from 2 to 8. Five of the nineteen pairs produced albino young, showing that they contained recessive albinism and transmitted it in approximately half their gametes, for the young produced by these pairs are 12 pigmented to 12 albino. Since the remaining fourteen pairs produced not a single albino in a total of 74 young, it is certain that many if not most of them did not form albino gametes, for had they done so half their young should have been albino. The albino parents used in this test evidently all transmitted latent the black-eyed character, for every one of the nineteen pairs produced dark-eyed young, showing that the albino parent was either of class (8), page 48, or possibly of class (7). The occurrence of an albino of this latter class (one which transmits latent in half its gametes the dark-eyed character, but in the other half the pink-eyed character) is shown beyond question, in Darbishire’s Table G, by a mating (2H 120) which produced 2 dark-eyed and 1 pink-eyed young. The occurrence of albinos which may have been either of class (7), page 48, or of class (9) (*i. e.*, which transmitted the pink-eyed character either in half or in all of their gametes) is indicated by three pairs in Darbishire’s Table F, page 36, as follows :

Pair.	Young.		
	$Pd.$	$Pp.$	$A.$
K 10. ....	1	2	...
K 11. ....	1	2	1
K 15. ....	...	2	3

In this experiment the parents both belonged to generation  $F_1$ , and were respectively a dark-eyed animal—which might be taken from any of the classes (1) to (4), p. 48—and an albino—which might be taken from any of the three classes (7) to (9). We should, on the theory of probabilities, expect half the eighteen pairs enumerated in Darbishire's Table F as producing pigmented young to produce pink-eyed offspring. Only three, as stated, gave this result, instead of the expected nine. But the number of young produced by several of the pairs was very small, being in four cases 3, and matings which should produce less than 1 in 4 of pink-eyed young (viz, 3 in 16) may well have failed to produce any in litters of 4 or less. In the three matings cited it is evident that both parents formed gametes bearing the pink-eyed character, since pink-eyed young were produced. Accordingly the dark-eyed parent must have belonged either to class (1) or to class (2), and the albino parent either to class (7) or to class (9). In mating K 10, the dark-eyed parent was probably of class (2), since no albino young were produced, though the small number of young, three, leaves this uncertain; but in matings K 11 and K 15, it is clear that the dark-eyed parent was of class (1), since albino young were produced in both cases. There is nothing to indicate whether the albino parents in these three matings were pure or hybrid as regards the pink-eyed character, except the large proportion of pink-eyed young produced, which would indicate that they were probably of class (9), *i. e.*, pure.

Accordingly, in Darbishire's experiments, we lack strong evidence by breeding test of the occurrence of this class (9) only of all those indicated on page 48. Yet I doubt not that the single albino born of pink-eyed parents, as recorded in Darbishire's Table H, page 37, if tested would prove to be of this sort, *i. e.*, lacking entirely the dark-eyed character, so that when mated with pink-eyed animals only pink-eyed offspring would be produced. This result would be parallel with what in mice Allen (: 04) observed to be the relation of chocolate and chocolate-yellow pigmentation to albinism, and what I, in guinea-pigs, have shown to be the relation of red and of yellow pigmentation to albinism.

#### HEREDITY OF ROUGH COAT.

In certain varieties of the domesticated guinea-pig the hair has a very peculiar arrangement, sloping away in all directions from certain points, which are situated for the most part symmetrically along the sides of the body, nearly coinciding with the centers of the typical pigment patches. As a consequence the animal seems covered with cowlicks or rosettes, between which the hair, sloping in opposite directions, forms a series of ridges or crests. These are best seen in the so-called Abyssinian (the short-haired but rough) variety. (See Pl. 2, figs. 3 and 4.)

When the rough coat character is best developed, rosettes are seen around the following paired centers: (1) The eye, (2) a point immediately behind the ear, (3) the shoulder, (4) a point dorso-lateral on the side of the body about midway between shoulder and hip, (5) the hip, (6) the groin, (7) each of the single pair of mammæ; and from two unpaired centers, viz, (8) the middle of the forehead, and (9) the navel. The direction of the hair is also reversed on the toes.

In crosses between pure rough individuals and smooth ones, the rough character is dominant, all the young being rough and ordinarily having the rough character as fully developed as in the rough parent. But certain smooth animals, which may properly be described as prepotent, produce offspring which show a weakened condition of the rough character, some of the typical rosettes being either less well developed than in the rough parent or wanting altogether (see Pl. 6, fig. 12). Such offspring may be called *partial rough*. They frequently transmit the rough character in its full intensity to their offspring, as we shall presently see, though they themselves are only partially rough.

Repeated crossing of rough animals with prepotent smooth ones results in further weakening of the rough character until it is almost eliminated. Successive stages in this weakening process may be recognized, which are about as follows:

Condition A: The fully developed rough character as above described (see Pl. 2, figs. 3 and 4).

Condition B: Forehead and shoulder rosettes have disappeared, hip and side rosettes either fuse into an obliquely longitudinal dorso-lateral part sloping downward posteriorly, or the hip center disappears entirely.

Condition C (Pl. 6, fig. 12): The only conspicuous rosettes are the side rosettes, though the ear rosettes may usually be found by careful examination; between the ear and side rosettes a ridge runs obliquely downward and backward across the body from the shoulder; there is likewise a median dorsal crest; the hair is reversed in direction on the hind feet, and turned laterally but not reversed on the front feet.

Condition D: Only a single pair of rosettes, the side rosettes, persist; a mid-dorsal crest extends from the head back to the rump; hair on the feet as in Condition C, or that of the front feet straight.

Condition E: No rosettes, a mid-dorsal crest from the head backward, perhaps half the length of the body; hair of toes reversed on hind feet only or not at all.

Condition F: No rosettes or crest. Hair reversed on hind feet only.

It must not be understood that these steps are necessarily taken one at a time. The original cross between rough and smooth may lead directly from Condition A to Condition D, when the smooth parent is very prepotent.



The matings which have been made between pure rough parents and smooth ones may be summarized as follows:

Parentage.	Young, in appearance.		
	<i>R.</i>	<i>PR.</i>	<i>Sm.</i>
<i>R.</i> ♂ 1516 × <i>Sm.</i> ♀ ♀ .....	12	5	...
<i>R.</i> ♂ 1586 × <i>Sm.</i> ♀ ♀ .....	8	...	...
<i>R.</i> ♂ 2002 × <i>Sm.</i> ♀ ♀ .....	113	11	...
<i>R.</i> ♀ 2040 × <i>Sm.</i> ♂ 2060.....	2	..	...
<i>R.</i> ♂ 2059 × <i>Sm.</i> ♀ ♀ .....	31	4	...
Total.....	166	20	...

[Abbreviations: *R.* = rough; *PR.* = partial rough; *Sm.* = smooth.]

It will be observed that every one of the 186 young produced by this experiment bears the rough character, all but 20 of them having it fully developed (Condition A); the character of the exceptional 20 partial-rough animals varies from Condition B to Condition D.

#### PREPOTENCY AND DOMINANCE.

The matings which produced the 20 partial-rough young are of particular interest. In detail they are as follows:

Parentage.	Young.		
	<i>R.</i>	<i>PR.</i>	<i>Sm.</i>
<i>Sm.</i> ♀ 208 (or 996?) × <i>R.</i> ♂ 2002.....	2	4	...
<i>Sm.</i> ♀ 2005 × <i>R.</i> ♂ 2002.....	...	5	...
<i>Sm.</i> ♀ 2005 × <i>R.</i> ♂ 2059.....	...	2	...
<i>Sm.</i> ♀ 2056 × <i>R.</i> ♂ 2002.....	4	2	..
<i>Sm.</i> ♀ 2056 × <i>R.</i> ♂ 2059.....	3	2	...
<i>Sm.</i> ♀ 1344 × <i>R.</i> ♂ 1516.....	1	3	...
<i>Sm.</i> ♀ 1499 × <i>R.</i> ♂ 1516.....	1	2	...

The partial-rough young, it will be noticed, were all produced by five (or possibly six) mothers. Unfortunately, there is some uncertainty as to the mother of the first of the lots of young enumerated. The two females (♀ 208 and ♀ 996) had 6 young together at the same time, and so it was impossible to separate the young by litters, but from the coloration and size of the young I think it probable that ♀ 208 was the mother of the 4 partial-rough young. But ♀ 996 was of the same smooth stock as ♀ 208, and it would not be surprising if her gametes had a similar potency. Unfortunately, no further tests with these mothers could be made, for they both died soon after producing the young enumerated. The two females, ♀ 2005 and ♀ 2056, were both mated with the same rough males (♂ 2002 and ♂ 2059). The former produced only partial-rough young by both males; the latter produced

some fully rough and some partial-rough young by both males. From these cases it seems clear that the production of partial-rough young was due to some unusual potency of the gametes bearing the smooth character, and that this potent character was inherent in *all* the gametes formed by ♀ 2005, but in only about *half* of those formed by ♀ 2056. If ♀ 208 was, as supposed, the mother of the 4 young, all partial-rough in character, then she probably formed only potent gametes, as did ♀ 2005 apparently; but if ♀ 208 and ♀ 996 each produced some of the partial-rough and some of the fully-rough young, then they were both similar in character to ♀ 2056, as regards the formation of potent gametes. It would seem probable, accordingly, that potency of the sort under consideration is a function of the gametes; that while most smooth females form *no* potent gametes, some form 50 per cent and some 100 per cent of such gametes; or, in other words, that some smooth animals are purely potent, others *hybrid*, as regards potency, but a majority *non*-potent.

The question now arises, is this potency handed on from generation to generation, *i. e.*, do the gametes remain pure as regards potency, or is their potency affected by a cross with the alternative and dominant character, rough coat. There is some evidence in favor of both these ideas. On one hand there is a manifest tendency for gametes to retain from generation to generation any abnormal potency which they may possess; but on the other hand cross-breeding probably does frequently alter the potency of recessive gametes.

The first of the two ideas just mentioned receives support from the admirable experiments of Coutagne (:02) with silk-moths, which seem to have received less attention than is warranted by their great richness in results and the care with which they have been executed. Coutagne crossed two distinct races of silk-moths, one of which produced only white cocoons, the other only yellow cocoons. Dominance apparently was alternative between the two characters, which seem to have been nearly equal in potency, so that sometimes one, sometimes the other dominated. The cocoons were 219 white in character, 240 yellow, without intermediates. Imagos hatching from either sort of cocoon, when mated *inter se*, produced the other sort of cocoon, as well as that from which they hatched, and approximately in the proportions 3 of their own sort to 1 of the other. Thus, moths hatching from white cocoons mated *inter se*, and moths hatching from yellow cocoons mated *inter se*, produced in different lots—

From white cocoons :

				TOTAL.
White .....	339	87	180	606
Yellow.....	140	36	109	285

From yellow cocoons :

White ..	120	34	80	234
Yellow .....	441	89	236	766

Evidently there is a strong tendency for white, when it dominates in a first cross, to behave as a dominant also among the progeny of that cross; and likewise for yellow, when it dominates in a first cross, to behave as a dominant among the progeny of that cross. This indicates clearly the persistence from generation to generation of relative potencies of gametes of a particular sort. As regards the relative proportions of white and of yellow cocooned young, it is noteworthy that there is throughout the experiment a slight excess of yellows over the expected, indicating a somewhat superior potency of that character, which, in matings between other white-cocooned and yellow-cocooned races, was found to be uniformly dominant.

That cross-breeding may modify the relative potencies of gametes seems highly probable, yet the evidence for this idea at present available is inconclusive. It consists principally in an observed excess of partial-rough young over the expected proportion in certain matings, which will presently be described, but the numbers of young as yet produced in these experiments are too small to be at all conclusive.

One mating of pure rough animals (*R.* ♂ 2002 × *R.* ♀ 2003) produced, as expected, only rough young, five in number (see p. 63).

Hybrid rough animals, *R.* (*Sm.*), when mated with pure rough animals, have produced, as expected, only rough young, 57 being fully rough (Condition A, p. 57) and 1 partial-rough (Condition B or C).

The one partial-rough animal occurred in a litter of three young borne by *R.* ♀ 2040 mated with hybrid *R.* (*Sm.*) ♂ 994. This female had previously borne two fully rough young by *Sm.* ♂ 2060 (see p. 58). It is probable, therefore, that the hybrid ♂ 994 did form some smooth gametes of unusual potency, though, unfortunately, he was not tested by other matings with rough females.

Hybrid rough animals, *R.* (*Sm.*) in character, when mated with smooth ones, have produced 127 rough young and 146 smooth ones, equality of the two classes being expected on the Mendelian hypothesis of segregation. Of the 127 rough young, all except 6 have Condition A, the fully rough coat. The 6 partial-rough young were produced in four different litters, each by a different pair. They were as follows:

Parentage.	Young, in appearance.		
	<i>R.</i>	<i>PR.</i>	<i>Sm.</i>
<i>R.</i> ( <i>Sm.</i> ) ♂ 1111 × <i>Sm.</i> ♀ 644.....	...	1	3
<i>R.</i> ( <i>Sm.</i> ) ♂ 1178 × <i>Sm.</i> ♀ 1661.....	1	1	...
<i>R.</i> ( <i>Sm.</i> ) ♂ 1332 × <i>Sm.</i> ♀ 1338.....	...	3	...
<i>R.</i> ( <i>Sm.</i> ) ♀ 2034 × <i>Sm.</i> ♂ 1147.....	...	1	1

The smooth animals used in these matings were all pure-bred except ♀ 1338, which had a hybrid, *R. (Sm.)*, father, but a pure-bred smooth mother. We can not assume, however, that these hybrid rough animals formed in general weak rough gametes, for *R. (Sm.)* ♂ 1111 had in all, by smooth females, 13 rough offspring, but only in the mating with ♀ 644 was a partial-rough individual produced; again *R. (Sm.)* ♂ 1178 had rough offspring (6 in all) by three different smooth females, but only in the mating with ♀ 1661 did he produce a partial-rough animal. It would seem that the degree in which dominance is realized in the zygote is dependent upon the relative potency of the gametes uniting, and that potency is apt to be more variable in the gametes of cross-bred than in that of pure-bred animals. If so, hybrid rough animals bred *inter se*, or with cross-bred rough or smooth individuals, should produce an especially large proportion of partial-rough young. The experiments made are as yet hardly extensive enough to give a decisive answer to this question.

Fully rough hybrid, *R. (Sm.)*, animals bred *inter se*, have produced in all 32 rough young, only one of which is a partial-rough. This one was produced by the following mating:

*R. (Sm.)* ♂ 1111 × *R. (Sm.)* ♀ 1438, produced 1 *R.*, 1 *PR.*, 2 *Sm.*

This same male, it will be remembered, produced a partial-rough individual by the smooth female 644.

We may return now to the question whether the condition of unusual potency in the smooth gametes of animals producing partial-rough young is handed on to the posterity of those animals. If the partial-rough character of hybrid animals is due simply to imperfectly realized dominance of the character borne by the dominant gamete, and if the characters united in the zygote maintain their distinctness and segregate with the same relative potencies, when gametes are formed by the hybrid as they possessed before, then we should expect to get fully rough, as well as partial-rough offspring, by mating partial-rough animals either *inter se* or with rough animals. The result of mating partial-rough with smooth animals would depend upon the relative potency of the gametes formed by the smooth mates; if *none* of their gametes were unusually potent, then the offspring should be half fully rough and half smooth, without partial-rough young. But if *half* the gametes formed by the smooth animals are unusually potent, then the offspring should be visibly as 1 *R.* to 1 *PR.* to 2 *Sm.*

Matings of these three sorts show the following results. The "expected" results are calculated on the hypothesis of persistent relative potencies and full segregation of the rough and smooth characters.

Parentage.	Young, in appearance.					
	Observed.			Expected.		
	<i>R.</i>	<i>PR.</i>	<i>Sm.</i>	<i>R.</i>	<i>PR.</i>	<i>Sm.</i>
<b>I.—<i>PR.</i> (<i>Sm.</i>) × <i>PR.</i> (<i>Sm.</i>):</b>						
♂ 1334 × ♀ 1267.....	...	2	1	...	...	...
♂ 1334 × ♀ 2029.....	1	2	...	...	...	...
♂ 1987 × ♀ 1268.....	1	2	1	...	...	...
♂ 1987 × ♀ 1269.....	...	1	2	...	...	...
♂ 1987 × ♀ 2007.....	...	3	...	...	...	...
♂ 1987 × ♀ 2008.....	2	...	2	...	...	...
Total.....	4	10	6	5	10	5
<b>II.—<i>PR.</i> (<i>Sm.</i>) × <i>R.</i> (<i>Sm.</i>):</b>						
♂ 1360 × ♀ 991.....	...	1	2	...	...	...
♂ 1360 × ♀ 1435.....	1	2	...	...	...	...
♂ 1631 × ♀ 1071.....	...	3	...	...	...	...
Total.....	1	6	2	4½	2½	2½
<b>III.—<i>PR.</i> (<i>Sm.</i>) × (<i>Sm.</i>):</b>						
♀ 1269 × ♂ 1024.....	...	1	2	...	...	...
♀ 1360 × ♀ 1327.....	...	1	1	...	...	...
♀ 1360 × ♀ 1506.....	1	...	3	...	...	...
♀ 1360 × ♀ 1595.....	1	...	...	...	...	...
♀ 1360 × ♀ 1596.....	...	1	1	...	...	...
♀ 1360 × ♀ 1859.....	...	1	1	...	...	...
♀ 1631 × ♀ 1029.....	1	...	...	...	...	...
♀ 1631 × ♀ 1035.....	...	...	2	...	...	...
♀ 1987 × ♀ 2107.....	...	...	3	...	...	...
♀ 1987 × ♀ 2119.....	1	...	...	...	...	...
Total.....	4	4	13	5½—10½	0—5½	10½

The agreement between the observed and the expected proportions of fully rough (*R.*) and partial-rough (*PR.*) offspring is sufficiently close to lend support to the hypothesis of persistent gametic potency from generation to generation. For on the alternative hypothesis, that partial-rough hybrid animals form only partial-rough gametes and smooth ones, no animals with the fully developed rough character should be formed either in Group I or Group III of the foregoing matings, but we see that young of this sort were produced in all these groups. Yet it is probable that cross-breeding must be recognized as an element which may modify the potencies of gametes, causing those of a cross-bred individual to be less uniform in potency than those of an animal not so crossed. Further experiments are needed to throw light on this question.

Leaving out of consideration the *degree* in which the rough character is developed in the coat of hybrid offspring, we may inquire how nearly the Mendelian proportions of rough and smooth young are approximated. This will be plain from an examination of the following table :

Nature of mating.	Young.			
	Observed.		Expected.	
	Rough.	Smooth.	Rough.	Smooth.
Rough $\times$ rough.....	5	...	5	...
Rough $\times$ rough (smooth).....	58	...	58	...
Rough $\times$ smooth.....	186	...	186	...
Rough (smooth) $\times$ rough (smooth).....	53	19	54	18
Rough (smooth) $\times$ smooth.....	135	159	147	147
Total.....	437	178	450	165
	615		615	

As in the case of albinism, there are a few more recessive individuals than are expected. This may be purely a chance result, or it may be due to superior fertility of the recessive gametes; but a different explanation is suggested by an observation which will presently be stated. The suggested explanation is that the excess of recessive individuals may be due to latency of the rough character in certain individuals apparently smooth. That such latency is possible is shown by the sudden appearance in one of my families of smooth animals of a partial rough individual, ♀ 969, having a well-marked crest extending from the head to the middle of the back and conspicuous though imperfectly developed side rosettes. The ancestors of this female for at least three generations had been ordinary smooth individuals, though it is possible that one or more of these may have had a slight crest in the region of the shoulders; for I found that a brother of ♀ 969, viz, ♂ 971, had such a crest, though it could be detected only by very careful examination. Unfortunately most of the ancestors had died before my attention was called to this case. The father's skin, which I have, shows no indication of a crest, though possibly it might have done so before it was dried. The partial-rough ♀ 969 had by the brother mentioned, ♂ 971, four young, one of which was a partial-rough like herself, the others being smooth. Clearly, then, she both possessed the rough character in a state of partial activity and was able to transmit it in this condition to her offspring, though in her ancestors it must have been present in a state of almost, if not quite complete latency. Very likely suitable matings of the mother would restore the rough character in certain of her offspring to a condition of full activity. Further experiments with this animal are now in progress.

If I have interpreted correctly the partial-rough animals obtained in my experiments, they may be similar in nature to centripetally pigmented animals which lack some of the typical pigment patches, or have only the eyes pigmented. A cross with albinos in which centripetal pigmentation is latent may serve to call the full set of coat spots into activity, producing fully pigmented young, as we have already seen. Similarly we may expect that crossing a partial-rough animal with a smooth animal in which the rough character is fully latent would call the rough character into full activity in the offspring. It remains, however, to demonstrate the existence of smooth animals containing *fully* latent the rough character. I have as yet no evidence of their existence other than the slight excess of smooth animals over the expected proportion.

#### HEREDITY OF LONG COAT.

The longest or contour hairs of ordinary domesticated guinea-pigs, like those of the wild *Cavia aperea*, do not exceed a length of about 4 centimeters, but domesticated varieties with hair many times that length are now well known. Where or when they originated is unknown; according to Cumberland they would seem to have been introduced into England from France; our American stocks probably came from England. Long-haired smooth animals are commonly called "Angoras," and long-haired rough ones "Peruvians." But the two sets of characters (long *vs.* short, and smooth *vs.* rough) are entirely independent of each other, as we shall see, so that for the present we shall consider only the length of the coat, irrespective of whether it is rough or smooth.

My first experience with long-coated guinea-pigs was wholly unpremeditated. In a family of short-haired guinea-pigs with which I was experimenting and was practicing close-breeding, there appeared several animals whose contour hairs were about twice as long as those of their parents. These animals were all descended from a single pair of short-haired guinea-pigs which had been purchased from a breeder, but which I have no doubt had numbered among their ancestors a long-haired animal. I found that the long-haired young bred true *inter se*, which indicated that the long-haired character was recessive in nature in relation to normal or short coat. This idea has been fully confirmed by subsequent experiments, which were systematically instituted with the longest haired animals which I could secure.

In studying the inheritance of this character, it is necessary to rear the young to an age of about two months before one can be sure whether they are to have a normal coat, or one of more than normal length. For at birth guinea-pigs of all sorts have hair of about the same length (2 cm.). The coat of short-haired guinea-pigs reaches its maximum length (about 4 cm.) not far from the age of one month, and

is then gradually shed. On the other hand, the hair of long-coated animals apparently is not shed at this period, but keeps on growing. At two months of age it is 5 to 7 cm. long, at three months it is 6 to 9 cm. long. In the period from three to four months of age is another critical stage. Animals which begin to shed their longest hair at this period apparently do not acquire a longer coat at any period of their subsequent life, but continue to have one whose maximum length is about 8 cm. But animals which pass the age of about four months without shedding their longest hairs increase the length of their coat rapidly, so that they may have a coat of 10 to 12 cm. maximum length when four to five months old, and one of 14 to 16 cm. at six to seven months.

The acquisition of an abnormally long coat is due, accordingly, not to unusually rapid growth of the hair, but to a peculiar mode of growth. The hairs of a normal animal are thick and stiff in the middle, but taper toward either end, somewhat like the quills of a porcupine. In the middle of the hair the medulla is very thick, but it diminishes gradually toward either end, where it is wanting altogether. A hair of this sort, then, is the result of a definite growth cycle in the hair follicle, this cycle covering apparently about two months' time, though my observations on this point are yet imperfect. When a hair is completed, after attaining a length of about 4 cm., a new one apparently is formed below it and crowds the old one out. But in the long-haired animal, the termination of a two-months growth cycle is frequently, if not regularly, omitted. The hair is more nearly of uniform thickness throughout its length, and is not narrowed to a base at the end of a single period of two months, but grows without interruption during two, three, or four such periods.

For this reason, as I have observed, hair measurements of long-coated animals do not form a continuous series, but tend to group themselves about mean maximal lengths as follows:

- (1) 8 cm., double the length of normal or short coat, not attained under three months of age.
- (2) 12 cm., three times the length of short coat; not attained under five months of age.
- (3) 16 cm., four times the length of short coat; not attained under seven months of age.

Coats longer than this I have not had an opportunity to study, though such are said to occur.

That long-haired animals bred *inter se* produce only long-haired young is shown by the following experiment: Six different long-haired males (viz, 955, 1586, Pl. 5, fig. 9, 1709, 2002, Pl. 1, fig. 1, and 2060, Pl. 3, fig. 5) have been mated with 19 different long-haired females, producing 49 young, all long-haired. There were produced also seven-



ral young which died before their coat-character could be determined, but all those which survived had hair much longer than that of the ordinary short-haired animal.

Further evidence of the recessive nature of long coat is afforded by matings between long-haired and short-haired animals. Long-haired ♂ 2002 (Pl. 1, fig. 1), whose coat measures 14–17 cm., according to condition, has been mated with 14 different short-haired females, producing 58 young, all of which have hair under 5 cm. in length. Nevertheless, the influence of the long-haired parent is frequently seen in increased softness of the coat, though this is, as a rule, not longer than in the short-haired parent.

When two long-haired animals are mated, one of which has longer hair than the other, the offspring have a coat like that of the shorter-haired parent, usually without, though sometimes with, interspersed hairs of greater length (Pl. 6, fig. 11). In other words there is a strong tendency for the shorter coat to dominate in all cases over the longer one. Accordingly, evidence for the dominance of short coat in crosses with long coat is fairly complete; the evidence for the occurrence of segregation in the next generation is less satisfactory, for, though there occur among the offspring good long-coated and good short-coated individuals, others show a poor development of the long coat, and the whole number of long-coated animals exceeds that expected. Thus hybrids, *Sh. (L.)\** in character, mated *inter se*, have produced thus far 13 *Sh.* to 7 *L.*, where 3 *Sh.* to 1 *L.* are expected, and long-haired animals when mated with hybrids, *Sh. (L.)*, for the most part children of ♂ 2002 (see Pl. 1, fig. 1) have produced 36 *Sh.* to 65 *L.*, or nearly twice as many long-haired as short-haired young, where equality of the two sorts is expected. These young have been born to seven different long-haired parents, and the excess of long-haired offspring appears among the young of all except two of them, as follows:

Parents.		Young.	
Long-haired.	Short-haired ( <i>Long</i> ).	Short.	Long.
♂ 206 .....	♀ ♀ — .....	5	5
♂ 732 .....	♀ ♀ — .....	5	9
♂ 1586 .....	♀ 1698 .....	0	4
♂ 1709 .....	♀ 1730 .....	2	1
♂ 2002 .....	♀ ♀ — .....	9	18
♀ 2040 .....	♂ 994 .....	0	3
♂ 2060 .....	♀ ♀ — .....	15	25
Total .....	.....	36	65

\* *L.* = long-haired, *Sh.* = short-haired.

The departure here from the expected equality of the two classes is too great and too uniform to be referable to chance. It would seem probable, rather, that fewer gametes are formed bearing the character short-coat than are expected. This may be due either to failure of contrasted characters to segregate at gamete formation in certain cases, or possibly to partial latency of the character short-hair in gametes which transmit active the character long-hair, the resultant being an intermediate condition. Further experiments are needed to show which of these two ideas is correct, though at present the former seems more probable.

Short-haired females obtained by mating a primary hybrid, *S* $\frac{1}{2}$  (*L*.), with a pure short-haired animal have, in several cases, been mated with the long-haired males, 2002 (Pl. 1, fig. 1) and 2060 (Pl. 3, fig. 5). It is expected that half of such females will contain recessive the character long-coat, and that half will be free from it, *i. e.*, will produce only short-haired young. The outcome shows that 9 out of 12 females tested contain recessive the character long-coat, for they produce long-coated young. This is another bit of evidence that segregation occurred less often than expected in the gametes of the primary hybrids, though it throws no doubt on the uniformly dominant character of short-coat. Again, the nine extracted hybrids, which contain recessive the character long-coat, should, when mated with long-haired animals, produce short-haired and long-haired young in equal numbers if segregation occurs in every case where it is expected. In the matings in question there have been produced 10 short-haired young and 16 long-haired ones—further evidence that segregation is less frequent than expected. It is true that these numbers are yet small, but their uniform deviation in one direction from the expected result indicates that they are significant. If so, we must recognize in this pair of characters full Mendelian dominance, attended, however, with only partial Mendelian segregation.

#### CORRELATION AMONG COAT-CHARACTERS.

In the preceding pages we have discussed separately the heredity of three different pairs of alternative coat-characters which we have found to conform more or less closely with Mendel's law of heredity. It remains to inquire whether there is any correlation between one of these pairs of characters and another, *i. e.*, whether rough coat is more often associated with white or with pigmented coat, with long or with short coat, etc. An inquiry of this sort may be based upon experiments made with the albino male 2002 (Pl. 1, fig. 1), which possessed the recessive members of two of the pairs of characters (*viz.* albinism and long-coat), but the dominant member of the third pair (*viz.* rough coat). It goes without saying that he was pure as regards albinism

and long-coat, for all long-haired albinos are pure in these characters, and as the result of experiment it may be stated that he was likewise pure as regards the third or dominant character, rough coat. He was mated with nine different pure pigmented, short-haired, and smooth females, producing 29 young, all pigmented, short-haired, and rough (see Pl. 2, figs. 3 and 4), but, presumably, all containing the three corresponding recessive characters—albinism, long coat, and smooth coat.

He was likewise mated with three other pigmented short-haired, smooth females, which differed from those previously mentioned only in this, that they contained recessive albinism. They produced by this mating 15 young, of which all, of course, were short-haired and rough, but 9 were albinos and 6 pigmented. The latter should be similar in nature to the 29 young of the matings previously described, making in all, from matings of ♂ 2002, 35 young bearing the three dominant characters, but supposed to contain the corresponding recessives, *i. e.*, to be hybrid in all three pairs of characters. A number of these young which were tested by suitable matings proved to be of the character expected. They have produced by different matings all the eight possible visibly different combinations of characters, viz :

- (1.) Pigmented rough short, *P. R. Sh.* (compare Pl. 2, fig. 4).
- (2.) Pigmented rough long, *P. R. L.* (compare Pl. 5, fig. 9).
- (3.) Pigmented smooth short, *P. Sm. Sh.* (compare Pl. 3, fig. 6).
- (4.) Pigmented smooth long, *P. Sm. L.* (compare Pl. 5, fig. 10).
- (5.) Albino rough short, *A. R. Sh.* (compare Pl. 2, fig. 3).
- (6.) Albino rough long, *A. R. L.* (compare Pl. 1, fig. 1).
- (7.) Albino smooth short, *A. Sm. Sh.* (compare Pl. 4, fig. 7).
- (8.) Albino smooth long, *A. Sm. L.* (compare Pl. 4, fig. 8).

This result shows clearly that there is no *necessary* correlation between either character of one pair and either character of another pair. On the hypothesis that each pair of characters is, in its transmission, *wholly* independent of the others, *i. e.*, that no correlation whatever exists among the pairs, we should expect triple hybrids, like the 35 young of ♂ 2002 already described, to produce, when mated *inter se*, young visibly of the eight different sorts just enumerated in the following proportions: 27 *P. R. Sh.*, 9 *P. R. L.*, 9 *P. Sm. Sh.*, 3 *P. Sm. L.*, 9 *A. R. Sh.*, 3 *A. R. L.*, 3 *A. Sm. Sh.*, 1 *A. Sm. L.* It will be noticed that at least 64 young must be reared to an age at which all three coat-characters can be determined before we may expect all these classes to be represented among the offspring. As yet only 8 young have been reared to such an age, so that the results are scarcely significant quantitatively, yet they indicate that the classes which are expected to be largest will really be so, for the eight young are distributed thus: 4 *P. R. Sh.*, 3 *P. R. L.*, 1 *P. Sm. Sh.*

Certain of the triple-hybrid offspring of ♂ 2002 were mated in ways

other than *inter se*, which should give some indication of whether any correlations exist among the three pairs of coat-characters. Thus triple hybrids were mated with several pure pigmented, smooth, and short-haired individuals, *P. Sm. Sh.*, as follows :

Parents.		Young.	
<i>P. (A.) R. (Sm.) Sh. (L.)</i>	<i>P. Sm. Sh.</i>	Rough.	Smooth.
♂ 2036.....	♀ 972.....	...	3
♂ 2036.....	♀ 973.....	2	1
♂ 2037..	♀ 906.....	3	...
♂ 2037.....	♀ 907 and 922....	3	...
♂ 2037.....	♀ 915.....	2	1
♂ 2037.....	♀ 933.....	1	2
♂ 2037.....	♀ —.....	...	1
♀ 2033-5.....	♂ 2061.....	4	5
Total.....	.....	15	13

All the young were, as expected, pigmented and short-haired. It is expected, further, that half will be rough, half smooth, and this result is approximated in the observed 15 rough to 13 smooth. The young, though visibly of only two sorts, should be—on the hypothesis that no correlations exist among the pairs of coat-characters—of eight different sorts, all equally numerous. For the gametes of the triple hybrids should be as follows: *P. R. Sh.* + *P. R. L.* + *P. Sm. Sh.* + *P. Sm. L.* + *A. R. Sh.* + *A. R. L.* + *A. Sm. Sh.* + *A. Sm. L.* But the gametes of the pure mates used should all be *P. Sm. Sh.*, and the zygotes formed (*i. e.*, the characters present in the young) should be with equal frequency of these eight sorts, parentheses indicating recessives not visible :

- |                                |                                     |
|--------------------------------|-------------------------------------|
| 1. <i>P. R. (Sm.) Sh.</i>      | 5. <i>P. (A.) R. (Sm.) Sh.</i>      |
| 2. <i>P. R. (Sm.) Sh. (L.)</i> | 6. <i>P. (A.) R. (Sm.) Sh. (L.)</i> |
| 3. <i>P. Sm. Sh.</i>           | 7. <i>P. (A.) Sm. Sh.</i>           |
| 4. <i>P. Sm. Sh. (L.)</i>      | 8. <i>P. (A.) Sm. Sh. (L.)</i>      |

The tests to determine what recessives each of the young possesses are not yet complete, but thus far show the following distribution :

- |                                |                                |
|--------------------------------|--------------------------------|
| Class 1. 1 (or 2) individuals. | Class 5. 1 individual.         |
| Class 2. 1 (or 2) individuals. | Class 6. 2 (or 3) individuals. |
| Class 3. 1 individual.         | Class 7. None.                 |
| Class 4. None.                 | Class 8. 4 individuals.        |

Considering that only ten individuals have as yet been fully tested, their distribution among the classes is sufficiently wide to indicate the probable absence of correlation among the three pairs of coat-characters. The full details of the several tests on which this classification of individuals is based will be given in a subsequent report when a larger number of tests has been completed.

## EXPERIMENTS WITH RABBITS.

Certain experiments with rabbits, while less extensive than those made with guinea-pigs, serve to confirm and extend some of the conclusions already reached.

## CROSS BETWEEN TWO DIFFERENT TYPES OF ALBINOS.

Particularly instructive are the experiments with two different types of albinos, the pure or wholly unpigmented type, and the Himalayan or peripherally pigmented type.

A pair of Himalayans purchased of a dealer produced in two successive litters only good Himalayan young, 12 in number. Presumably, therefore, they were pure.

A pure white female rabbit born of pigmented parents, but herself wholly unpigmented, was likewise found to breed true when mated to animals like herself. Crosses were now made between the two breeds, as follows :

Parents.		Young.		
Pure white.	Himalayan.	Dark Himalayan.	Intermediate.	Mosaic.
♀ 1.....	♂ 6.....	2	3	1
♀ 1.....	♂ 7.....	1	2	3
Total.....	.....	3	5	4

All the young had pigmented extremities ; some were nearly or quite as heavily pigmented as those of the Himalayan parent, but others had pigmentation less heavy than that of the Himalayan parent ; these we may call intermediate. Still others bore pigment on part only of the areas which are pigmented in a pure Himalayan ; thus the foot might be pigmented, but its toes pure white, or the center of the nose white, with a sooty band lying above and to either side of it. Individuals such as this we may call mosaics. Dominance of the peripheral pigmentation was, accordingly, very imperfectly realized in the hybrid offspring. Nevertheless, segregation of the two types of albino character involved in this cross takes place with great regularity when the hybrids form gametes, and this is true alike of all three sorts of young, the dark Himalayan, the intermediate, and the mosaic, as the following matings show.

Parents.		Young.			
Hybrid.	Pure white.	Dark Himalayan.	Intermediate mosaic.	Intermediate.	Pure white.
Dark Himal'n ♀ 24.	♂ 56. ....	...	2	...	2
Mosaic ♂ 20.....	♀ 1.....	...	1	2	3
Intermediate ♂ 19...	♀ 51.....	1	...	2	2
Total .....	.....	1	3	4	7
		8			

The observed result approximates equality of the pigmented and unpigmented classes of albinos, as expected on the hypothesis that segregation occurs in all cases. The one good Himalayan produced by the intermediate ♂ 19 is noteworthy as showing that the full Himalayan character was present in the hybrid and capable of segregation, though seen in a partially dominated condition in the hybrid himself. Similar cases occur in the matings enumerated below. Apparently cases of this sort are like those of the imperfect rough guinea-pigs produced by certain smooth animals in crosses with rough ones, which nevertheless were capable of transmitting the rough character in its full intensity.

Further evidence of segregation of the Himalayan and pure white types of albino character in the gametes of the hybrids is afforded by mating these *inter se*, as the following experiments show.

Parents.		Young.				
Hybrid.	Hybrid.	Himalayan type.				P.
		D.	D. M.	I. M.	I.	
I. ♂ 19.....	I. ♀ 21.....	1	1	1	4	...
I. ♂ 19.....	D. ♀ 23.....	...	...	...	1	...
I. ♂ 19.....	D. ♀ 24.....	2	...	2	...	3
D. M. ♂ 20.....	I. ♀ 21.....	1	1	2	...	3
D. M. ♂ 20.....	I. ♀ 22.....	2	...	3	3	1
D. M. ♂ 20.....	D. ♀ 23.....	3	1	...	...	...
		9	3	8	8	7
		28				
D. M. ♂ 20.....	I. ♀ 21.....	6				1
I. M. ♂ 45.....	D. M. ♀ 108....	3				3
I. M. ♂ 45.....	D. ♀ 109.....	5				1
Totals observed.....		42				12
Totals expected .....		40½				13½

*Explanation.*—D. = fully pigmented or dark Himalayan; D. M. = dark mosaic; I. M. = intermediate mosaic; I. = intermediate; P. = pure white.

The observed numbers of Himalayan and pure white young, it will be noticed, approximate fairly well the numbers expected on the hypothesis of complete segregation.

The possibility of transmuting the Himalayan type into the pure white type by cross-breeding is suggested by an interesting experiment performed by Raspail (: 02). He set at liberty in a park frequented by wild gray rabbits, a Russian female rabbit, which variety has the Himalayan type of peripheral pigmentation. The female was presumably fertilized by wild males, certainly by pure pigmented animals, as the outcome indicates. In three successive litters she produced only self-colored gray or black young, in numbers approximately equal, as follows:—

	Gray.	Black.
Litter 1 ....	7	6
Litter 2.....	8	4
Litter 3 .....	3	6
Total.....	18	16

Certain of the gray hybrids bred *inter se* produced 5 gray young, 3 white ones [apparently Himalayan], and 1 *pure white*. Two of the [Himalayan] whites, when mated *inter se* produced a litter of 4 [Himalayan] white young. Two of these in turn interbred produced 5 *pure white* offspring.

This experiment I attempted to repeat, substituting for the wild pigmented parent a pure reddish gray pigmented animal of the breed known as the Belgian hare. A female Belgian hare was mated with Himalayan ♂ 6, the original male employed in the experiments already described. Three young were reared, a male and two females, of a gray color somewhat darker than that of the mother, since it contained more black pigment. The hybrids bred *inter se* have produced young as follows:—

Parents.	Young.		
	Gray.	Black.	Himalayan.
♂ 48 × ♀ 49.....	2	(4?)*	3
♂ 48 × ♀ 50.....	5	1	1
♂ 48 × ♀ 50.....	5	3	2
Total.....	20		6

\* Gray or black, died early.

It is expected that one-fourth of the young will be albinos, and this proportion is approximated. But all six of the albinos thus far obtained have pigmented extremities, as did their Himalayan grandfather. No pure whites have been produced. In this respect my results differ from those of Raspail. It is true that the intensity of pigmentation of these extracted Himalayans varies considerably, as does that of the pigmented young. There are dark and light Himalayans, just as there are dark and light grays, among the offspring. Cross-breeding has in this case, as in others, been the cause of variation within the types of the parents, but I have no evidence as yet that it can completely remove the pigmentation from the Himalayan albino type, thus converting it into a pure albino. Nevertheless further experiments may lead to this result, yet I hardly expect it in view of the distinctness shown by the Himalayan and the pure albino types in the experiments already described. I suspect, rather, that the Russian female, with which Raspail began his experiments, was in reality a hybrid, like those which I have described on page 70, in which *pure* albinism was recessive. Raspail says concerning her, page 172 :

La femelle de Lapin russe qui m'a servi pour mes expériences, n'était pas de race pure : le museau, l'extrémité des pattes, les oreilles et le dessus de la queue étaient d'un noir moins franc et moins velouté ; sa taille était notablement plus forte et ses yeux rouges indiquaient qu'elle tournait à l'albinisme.

This explicit statement and description certainly favors the idea that she was a cross-bred with a *pure* albino race, which, if true, would fully explain the occurrence of pure albinos in her offspring of generation  $F_2$ , without necessitating the conclusion that the peripherally pigmented type of albino had been transmuted into the unpigmented type by cross-breeding.

#### HEREDITY OF LONG OR "ANGORA" COAT.

This character is in rabbits, as in guinea-pigs, a recessive Mendelian character. Dominance and segregation both appear to be complete in crosses between normal (or short-haired) and angora (or long-haired) rabbits. I have observed in this case neither formation of intermediates, *i. e.*, of inferior long-haired specimens, nor deviation from the expected proportions of long-haired and short-haired individuals, of which conditions there were some indications in guinea-pigs. But in one or two cases I have thought that I could recognize in hybrids a greater softness of the coat, just as in guinea-pigs which are cross-breds between long-haired and short-haired races.

The numbers of young thus far reared are small, and not much weight is to be attached to them, so far as quantitative results are concerned.



In detail the matings made are as follows :

Parents.		Young.	
Long.	Short.	Short.	Long.
♂ N.....	♀ ♀ 17, 18, and 28..	10	...
♂ 45.....	♀ Lop.....	8	...
Total.....	.....	18*	...
Short (L.)	Short (L.)	Short.	Long.
♀ 1.....	Brother.....	4	2
♀ 1.....	♂ 20 (son) .....	5	1
♀ 21.....	♂ 20.....	6	2
Total.....	.....	15†	5
Long.	Short (L.)	Short.	Long.
♂ 45.....	♀ 108.....	2	4
♂ 35.....	♀ 109.....	4	2
Total.....	.....	6‡	6

\* Expected, all short.

† Expected, 3 short : 1 long.

‡ Expected, 1 short : 1 long.

EXPLANATION.—L. = long-haired or angora. Parentheses indicate recessive characters not visible.

#### HEREDITY OF LOP-EARS.

Some experiments are likewise in progress with the inheritance of the large or lop-eared character in rabbits, but these are hardly far enough advanced to make their outcome certain. The young produced by a cross between two breeds having ears of different relative size themselves have ears of an intermediate size. In other words, there is no evidence of dominance. A second generation of young has been obtained, but is not yet fully grown ; apparently they too will have ears of an intermediate character. If so, we may conclude that segregation as well as dominance is wanting in this case, which would seem to be one of blended or non-Mendelian inheritance, similar to that of the willow-hybrids studied by Wichura and that of the Hieracium hybrids of Mendel ('70).

## SUMMARY.

(1) There occur among domesticated guinea-pigs three pairs of alternative coat-characters which conform in their inheritance to Mendel's law of heredity. These are (1) albinism, which is recessive with respect to pigmented coat; (2) smooth coat, which is recessive with respect to rough coat; and (3) long coat, which is recessive with respect to short coat. Two of the recessive characters, viz, albinism and long coat, are doubtless characters of comparatively recent origin, which have made their appearance since the guinea-pig was domesticated. The third recessive character, smooth coat, is undoubtedly ancestral, and curiously enough is regularly dominated by rough coat, a character probably of recent origin, for a cavy bearing rosettes like those of the "Abyssinian" guinea-pig is unknown in a wild state. This indicates that ancestral characters are not necessarily dominant over new characters in heredity. The three pairs of characters are probably wholly uncorrelated.

(2) In rabbits occur two of the three pairs of alternative coat-characters which are found in guinea-pigs. Here, too, albinism and long or "angora" coat are recessive characters. A rosetted or rough coat is unknown in rabbits.

(3) A sharp distinction must be made between characters which are recessive and those which are latent. Recessive characters disappear from an individual in which they are associated with the corresponding dominant character, yet they reappear distinct in half the gametes formed by that individual; latent characters are characters normally dominant, which have disappeared in recessive gametes beyond hope of recall, except under conditions of cross-breeding which are in most cases not entirely clear. Albino gametes transmit in a latent condition both specific pigment characters and specific color-patterns. These latent characters can be brought into activity only by cross-breeding with a pigmental animal. The rough coat-character may likewise become almost completely, if not quite completely, latent in smooth animals. These facts indicate a possible explanation of the observed slight excess of recessives over the Mendelian expectation in cases involving one or the other of these two pairs of characters. In the case of the long *vs.* short pair of characters, an excess of recessives and the occurrence simultaneously of intermediates in generation  $F_2$ , but not in  $F_1$ , are more probably due to imperfect segregation than to latency of the dominant character. It is possible, however, that *partial* latency and imperfect segregation are related, if not identical phenomena.

(4) Some recessive individuals are prepotent, for their gametes, when united with those of ordinary dominants, produce young of an intermediate character. These intermediates, however, have the power to transmit the full dominant character in matings with recessive individuals. There is reason to believe, accordingly, that the dominant character is in such cases, not partially latent, but partially *dominated*. If so, we have in cases of this sort something remotely resembling the alternative dominance seen in certain of the crosses among silk moths made by Coutagne (: 02).

(5) The lop-eared condition in rabbits is probably a non-Mendelian character in its relation to normal ear; for the children and grandchildren produced by crosses are apparently alike intermediate in character.

(6) A cross between two different types of albino rabbits, Himalayan and pure white, shows imperfect dominance of the Himalayan character in the offspring, but complete segregation among their gametes.

(7) Cross-breeding between dominant and recessive individuals may lead to the production of new sorts of individuals in a variety of ways, *e. g.*, (1) by producing new combinations among different pairs of alternative characters, as among the children of triple-hybrid guinea-pigs; (2) probably by causing a complex character, like the agouti coat of guinea-pigs, to break up into its elements—black, chocolate, and yellow—one or more of the elementary pigment characters either becoming latent or passing bodily out of the gamete; (3) by the coming into activity of elements of the dominant character which were latent in recessive gametes, as black latent in albino guinea-pigs or in Himalayan rabbits (see next report); (4) by inducing variability in the intensity of characters, quite aside from resolution and recombination of characters, as when red cross-bred with black produces a very light shade of red, *e. g.*, yellow or cream.

## BIBLIOGRAPHY.

Allen, G. M.

- :04. The heredity of coat color in mice. *Proc. Amer. Acad. Arts and Sci.*, vol. 40, no. 2, pp. 61-163, 7 figs.

Bateson, W.

- :02. Mendel's principles of heredity, a defence. With a translation of Mendel's original papers on hybridisation. xiv + 212 pp. Cambridge. [England. Contains bibliography and portrait of Mendel.]

Bateson, W.

- :03. The present state of knowledge of colour-heredity in mice and rats. *Proc. Zool. Soc. London*, 1903, vol. 2, pp. 71-99.

Castle, W. E.

- :03. Mendel's law of heredity. *Proc. Amer. Acad. Arts and Sci.*, vol. 38, no. 18, pp. 535-548.

Castle, W. E.

- :03a. Mendel's law of heredity. *Science*, n. s., vol. 18, No. 456, pp. 396-406, September 25, 1903. [A reprint of the foregoing, with some additions and corrections.]

Castle, W. E.

- :03b. The laws of heredity of Galton and Mendel, and some laws governing race improvement by selection. *Proc. Amer. Acad. Arts and Sci.*, vol. 39, no. 8, pp. 223-242.

Castle, W. E.

- :03c. The heredity of "Angora" coat in mammals. *Science*, n. s., vol. 18, no. 467, pp. 760-761, December 11, 1903.

Castle, W. E., and Allen, G. M.

- :03. The heredity of albinism. *Proc. Amer. Acad. Arts and Sci.*, vol. 38, pp. 603-622.

Coutagne, G.

- :02. Recherches expérimentales sur l'hérédité chez les vers à soie. *Bull. Sci. France et Belg.*, tom. 37, pp. 1-194, pls. 1-9.

Cuénot, L.

- :03. L'hérédité de la pigmentation chez les souris. (2<sup>me</sup> note.) *Arch. Zool. Expér. et Gén.*, sér. 4, tom. 1, Notes et Revue, pp. xxxiii-xli.

Cuénot, L.

- :04. L'hérédité de la pigmentation chez les souris. (3<sup>me</sup> note.) *Arch. Zool. Expér. et Gén.*, sér. 4, tom. 2, Notes et Revue, pp. xlv-lvi.

Cumberland, C.

- [Date?] The guinea-pig, or domestic cavy, for food, fur, and fancy. 100 pp., illus., London. L. Upcott Gill.

Darbishire, A. D.

- :03. Third report on hybrids between waltzing mice and albino races. *Biometrika*, vol. 2, pt. 3, pp. 282-285.

Darbishire, A. D.

- :04. On the result of crossing Japanese waltzing with albino mice. *Biometrika*, vol. 3, pt. 1, pp. 1-51, 8 figs.

Galton, F.

- :97. The average contribution of each several ancestor to the total heritage of the offspring. *Proc. Roy. Soc.*, London, vol. 61, pp. 401-413.

Guaita, G. von.

- :98. Versuche mit Kreuzungen von verschiedenen Rassen des Hausmaus. *Ber. naturf. Gesellsch. zu Freiburg*, Bd. 10, pp. 317-332.

**Guaita, G. von.**

- :00. Zweite Mittheilung über Versuche mit Kreuzungen von verschiedenen Rassen des Hausmaus. Ber. naturf. Gesellsch. zu Freiburg, Bd. 11, pp. 131-138, 3 Taf.

**Haacke, W.**

- '95. Ueber Wesen, Ursachen und Vererbung von Albinismus und Scheckung, und über deren Bedeutung für vererbungstheoretische und entwicklungs-mechanische Fragen. Biol. Centralbl., Bd. 15, pp. 44-78.

**Loeb, L.**

- '97. Ueber Transplantation von weisser Haut auf einem Defect in schwarzer Haut und umgekehrt am Ohr des Meerschweinchens. Arch. Entw.-Mech., Bd. 6, pp. 1-44. 3 Taf., 2 Fig.

**Mendel, G.**

- '66. Versuche über Pflanzenhybriden. Verh. Naturf. Vereins in Brünn, Bd. 4, Abh., pp. 3-47. [Translation in Bateson, :02.]

**Mendel, G.**

- '70. Ueber einige aus künstlicher Befruchtung gewonnenen Hieracium-Bastarde. Verh. Naturf. Vereins in Brünn, Bd. 8, Abh., pp. 26-31. [Translation in Bateson, :02.]

**Pearson, K.**

- :04. A Mendelian's view of the law of ancestral inheritance. Biometrika, vol. 3, pt. 1, pp. 109-112.

**Raspail, X.**

- :02. Note sur une race de lapins albinos issue du croisement d'une femelle de lapin russe et d'un male garenne (*Lepus cuniculus*). Bull. Soc. Nat. d'Acclimatation de France, 49<sup>me</sup> année, pp. 170-175.

**Shaw, T.**

- :03. The study of breeds in America. Cattle, sheep, and swine. xvi + 371 pp., illus. Orange Judd Co., N. Y.



FIG. 1.—A LONG-HAIRED, ROUGH, ALBINO GUINEA-PIG, ♂ 2002.

Pure (*i. e.*, homozygous) as regards all three coat-characters, two of which are recessive in nature, one dominant. Fanciers' name for all animals of this appearance, whether homozygous or heterozygous in character, White Peruvian.



FIG. 2.—A SHORT-HAIRED, SMOOTH, RED GUINEA-PIG, ♀ 1355.

Pure in respect to two of its coat-characters, viz, smooth coat and pigmented coat, but heterozygous as regards the third, since it contains recessive long coat, though its own coat is no longer than that of most pure short-haired animals. Toes of right fore foot white. Fanciers' name for animals of this appearance, whether or not homozygous, Red English.





FIG. 3.—A SHORT-HAIRED, ROUGH, ALBINO GUINEA-PIG, ♂ 1095.

Son of ♂ 2002 (fig. 1, pl. 1) and of Red English ♀ 3, which contained recessive albinism, but was otherwise homozygous (compare fig. 2, pl. 1). This animal is a double heterozygote, containing recessive the two characters, long coat and smooth coat. As regards albinism, it is, of course, pure. Fanciers' name for all animals of this appearance, White Abyssinian.



FIG. 4.—A SHORT-HAIRED, ROUGH, BLACK-RED PIGMENTED GUINEA-PIG, ♂ 2037.

Son of ♂ 2002 (fig. 1, pl. 1) and of *pure* Red English ♀ 755 (compare fig. 2, pl. 1). A triple heterozygote containing recessive the three characters, long coat, smooth coat, and albino coat. The black pigment seen in this animal's coat was inherited, not from the red pigmented mother, but from the albino father. Unfortunately black areas are scarcely distinguishable from red ones in the figure. Fanciers' name for all animals of this appearance, Tortoise-shell Abyssinian.







FIG. 5.—A LONG-HAIRED, SMOOTH, ALBINO GUINEA-PIG, ♂ 2060.

From inspection alone of this animal, one may know that it is pure as regards coat-characters, since it manifests the three which are by nature recessive. Fanciers' name, White Angora.



FIG. 6.—A SHORT-HAIRED, SMOOTH, RED-BLACK PIGMENTED GUINEA-PIG.

The parents were both triple heterozygotes (compare fig. 4, pl. 2). This animal is, of course, pure as regards smooth coat, but whether it contains the two recessive characters which it does *not* manifest, can be determined only by breeding tests. In this figure, as in fig. 4, black areas unfortunately are indistinguishable from red ones. Fanciers' name for all animals of this appearance, whether pure or heterozygous, Tortoise-shell English.





FIG. 7.—A SHORT-HAIRED, SMOOTH, ALBINO GUINEA-PIG, ♀ 1499.

Daughter of two albino parents, viz, ♀ 99T, a double heterozygote like ♂ 1095 (fig. 4, pl. 2), and ♂ 635, a pure short-haired, smooth animal. We know without experimental test that this animal is pure as regards the two recessive characters which it manifests, smooth coat and albinism, but breeding tests are necessary to show whether or not it contains recessive the character long coat. This animal has been found to form *prepotent* smooth gametes. Fanciers' name for all animals of this appearance, White English.



FIG. 8.—A LONG-HAIRED, SMOOTH, ALBINO GUINEA-PIG, ♀ 1756.

Daughter of ♂ 2060 (fig. 5, pl. 3) and of ♀ 993, which was a double heterozygote like ♂ 1095 (fig. 3, pl. 2). This animal, like ♂ 2060, being a triple recessive, is pure as regards all three coat-characters. Fanciers' name, White Angora.





FIG. 9.—A LONG-HAIRED; ROUGH, BLACK-WHITE SPOTTED GUINEA-PIG, ♂ 1586

Son of ♂ 2002 (fig. 1, pl. 1) and of ♀ 1067, which was a spotted triple heterozygote (compare fig. 4, pl. 2). We know without breeding tests that this animal is pure as regards the character long coat, the recessive which it manifests. Breeding tests have established the fact that it is pure also as regards the rough character, but heterozygous as regards pigmented coat, since it produces albino offspring when mated to albinos. Fanciers' name for all animals of this appearance, "Broken-color" Peruvian.



FIG. 10.—A LONG-HAIRED, SMOOTH, SPOTTED AGOUTI-RED-AND-WHITE GUINEA-PIG, ♂ 1709.

Son of ♂ 2060 (fig. 5, pl. 3) and of ♀ 1105, a triple heterozygote (compare fig. 4, pl. 2). This animal manifests two recessive coat-characters, long coat and smooth coat, in regard to which it is, of course, pure, but it is heterozygous in respect to the third pair of coat-characters, for it produces albino as well as pigmented offspring, when mated to albinos.





FIG. 11.—A PARTIALLY LONG-HAIRED, ROUGH, AND SPOTTED GUINEA-PIG, ♀ 2258.

Daughter of two triple-heterozygotes (compare fig. 4, pl. 2). The long-haired character is imperfectly developed in this animal, only *part* of the hair being long as in the Peruvian grandparent, ♂ 2002 (fig. 1, pl. 1).



FIG. 12.—A TRIPLE HETEROZYGOTE, ♂ 1989<sup>a</sup>.

(Compare fig. 4, pl. 2.) Son of ♂ 2002 (fig. 1, pl. 1) and of black-eyed white ♀ 2005, which is also a prepotent smooth animal. The coat is in part pigmented; the rough character is imperfectly developed, showing only one pair of the rosettes which are typically formed (compare figs. 3 and 4, pl. 2).









# MUTANTS AND HYBRIDS OF THE OENOTHERAS.

BY

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PLATE I.



Cultures of Oenotheras in the New York Botanical Garden.

*Onagra lamarckiana* at left in second row; *O. argillinea* in foreground, first row; *O. rubrinervis*, center second row; *O. lamarckiana* × *O. blennis* at right (a.24, a.32, and a young plant of a.1 emerging from the rosette stage).

# MUTANTS AND HYBRIDS OF THE OENOTHERAS

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## PURPOSE AND SCOPE OF INVESTIGATIONS.

The more important features of the investigations of De Vries in which lines of descent were seen to originate, which embodied new qualities and groupings of characters, constant and fully transmissible, are now so familiar to all naturalists that no rehearsal is necessary in the present paper. Early in 1902 the senior author received seeds of the Lamarck's evening-primrose, and these, with seeds of various species obtained directly from their native habitats in North America, were cultivated in the New York Botanical Garden, in which the conditions of soil and climate are, of course, widely different from those of the botanical garden at Amsterdam, Holland.

Among other primary purposes of the cultures it was deemed of great importance that the mutants should be tested as to their stability when grown as biennials after the predominant habit of the genus. The results of this test, together with detailed descriptions of three of the mutants, have already been given in an article in which occasion was taken to set forth briefly the principal tenets of the mutation theory as propounded by De Vries (MacDougal, 1903). It was found that the mutant forms were not only physiologically differentiated, but were also easily separable from one another and from the parental type when tested by accepted taxonomic criteria, and by an examination of the features of their life-histories. Furthermore, all the forms came true to their newly assumed groupings of characters without reversions, and

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\*The contents of this paper were presented before the weekly botanical convention at the New York Botanical Garden, October 19, 1904.

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exhibited only fluctuating variations of ordinary amplitude, although the last-named feature was not examined by statistical methods. An investigation of this feature is described in the present paper.

During the earlier cultures, plans were formulated for a somewhat inclusive investigation of the genetic relationships of the various members of the genus, and of the variations, or mutations, which might be found to occur in *O. lamarckiana* in America, and in the other species of the group. To this end correspondence was established with collectors in various parts of America and Europe, and material was obtained from such distant points as New Zealand, Mexico, Holland, and Japan. A supply of paraffined paper bags was furnished by Professor De Vries, and later those manufactured for the Station for Experimental Evolution at Cold Spring Harbor were used for inclosing the inflorescences, by which absolutely pure crops of seeds of the species, as well as of the various hybrids, were obtained. All sowings of seeds were made in soil sterilized in an autoclav for three or four hours. A number of the parcels of earth treated in this manner were moistened and kept under proper conditions, but in no instance were any germinations of other oenotheras seen. In order to economize time it was found most convenient to grow the evening-primroses as annuals, which may be done by germinating the seeds in a propagating house and then transplanting them to the experimental grounds early in May. The earlier cultures were begun about January 1, but it was found that ample time for the entire development of the plant was obtained if the sowings were made late in February or early in March.

The portions of the general investigation in which such progress has been made as to warrant the publication of the present paper are as follows:

(1) Determination of the ancestral habitat and dissemination of *Onagra* (*Oenothera*) *lamarckiana*.

(2) Description of such species of *Onagra* (*Oenothera*) as have been kept under cultivation for one or two seasons in order to facilitate observation of possible mutants.

(3) Analysis of the relationship between *O. lamarckiana* and other species of the genus by means of hybridizations.

(4) Estimation of the dominance of parental characters in hybrids of *O. lamarckiana*  $\times$  *O. biennis* and *O. lamarckiana*  $\times$  *O. cruciata*.

(5) Determination of the recurrence and stability of mutants of the oenotheras; description of *O. gigas* as cultivated in the New York Botanical Garden.

(6) Estimation of the fluctuating variability of some of the characters of *O. lamarckiana*, *O. nanella*, and *O. rubrinervis*.

PLATE II.



Large-flowered Evening Primrose, figured in Barton's Flora of North America,  
resembling *Onagra lamarckiana*.



## DERIVATION OF ONAGRA (OENOTHERA) LAMARCKIANA.

As a result of the earlier examination of material in a few herbaria in Europe and America no specimens of *O. lamarckiana* were found that had been grown in America, and it was suggested that it might have been originally native to a restricted range in Virginia from which it had been exterminated. The inquiry upon this phase of the investigation has been continued however, with the result that many historical records, as well as some fairly well authenticated material, have been found.

Barton (1821) describes an *oenothera* under the name of *O. grandiflora* in his Flora of North America, which, with the accompanying plate, well represents *O. lamarckiana*. (Pl. II.) This plant is described as "native in the woods and fields, and about habitations, in Carolina and Georgia, flowering from May to August." The fact is recalled by Barton that Elliott restricted the habitat of this form "to the vicinity of habitations in South Carolina and Georgia, remarking that it is certainly not indigenous in the low country."

Pursh (1814) had previously described an *O. grandiflora* similar to that mentioned by Bartram, as "in woods and fields of Carolina," and with "flowers larger than any other of the North American species, and of an agreeable scent."

The Floral Magazine for 1862 gives a plate of *Oenothera lamarckiana* with some notes on the species from which the following is quoted: The one now figured was grown by Messrs. Carter & Co., the well-known seedsmen of High Holborn and of the Crystal Palace nursery, Forest Hill. To them we are indebted for the following particulars (Dombrain, 1862):

We received, about four years ago, some seed from Texas unnamed. When we had flowered it we sent some blooms to Dr. Lindley, who pronounced it to be *Oenothera lamarckiana*, a species we believe introduced into England by Mr. Drummond. Its height is between 3 and 4 feet; it blooms the first year, is a very hardy biennial, and is superior to any other *Oenothera* in the size and number of its blossoms, which measure 4 inches in diameter.

A reproduction of the same plate is to be found in L' Illustration Horticole for 1862, together with a discussion of the origin and relationships of the various species and a citation of the statements quoted above. (Lemaire, 1862.)

A specimen in the Gray Herbarium of Harvard University was examined which agrees perfectly with *O. lamarckiana*. From the inscription, which is in Dr. Asa Gray's handwriting, it appears that this plant was grown from seed in the botanical garden at Cambridge, Mass., in 1862. The sheet also bears the note, "Said by English hor-

ticulturists to come from Texas," and also "*Oe. lamarckiana*," all by Dr. Gray. It is to be noted that the date of the above culture agrees with that of the Drummond plants in England mentioned above.

The second phase of the effort to trace *O. lamarckiana* to its original habitat was directed to an examination of the material to be found in the American herbaria and to excursions to some of the historical locations. Several specimens of prime interest were encountered. A specimen collected by A. W. Chapman in Florida, and sent by him to Europe, becoming a part of the Meissner herbarium which was afterward purchased by Columbia University, was thought by Professor De Vries to be *O. lamarckiana*, and the mark on the sheet shows that it was used by Chapman (1860, 1872, 1884) in making up the description of *O. biennis* in the editions of his southern flora, in which *O. grandiflora* Ait. was given as a synonym in the editions of 1860 and 1862, but does not appear in the later edition of 1897. In the description he says: "Varies greatly in pubescence and size of flower," while the habitat is given as "Fields and waste places." The elimination of the synonym from the last edition of the book can not be accounted for, although the plant was presumably growing in a wild condition. A duplicate of the specimen mentioned above is reported by Mr. C. D. Beadle to be in the Biltmore Herbarium at Biltmore, N. C. A similar specimen is to be found in the herbarium of the Missouri Botanical Garden.

During the visit of Professor De Vries to America in the summer of 1904 he joined in the quest for specimens of *O. lamarckiana* and called attention to a sheet of material in the herbarium of the Philadelphia Academy of Sciences, collected by C. W. Short near Lexington, Ky., which he considered as *O. lamarckiana*, and which was grown wild in the locality recorded.

The co-operation of a number of botanists in various parts of the supposed range of the species was secured and a thorough search was made in the vicinity of Nashville, Tenn., by Prof. Geo. A. Martin; in the vicinity of Knoxville, Tenn., by Prof. S. M. Bain; in the vicinity of Lexington, Ky., by Prof. H. Garman; and in the vicinity of Courtney, Mo., by Mr. B. F. Bush. Up to the present time, however, no living plants have been found that might be included within the descriptions of *O. lamarckiana*.

The above evidence makes it fairly conclusive, however, that the large-flowered evening-primrose which formed the basal material for the experimental researches of De Vries is, or was, a component part of the flora of North America and has been seen in the Carolinas, Florida, Kentucky, and Texas during the last century, and that material from Texas examined by Lindley fairly represents the

species. The main line of descent has endured practically unchanged for a period of 116 years in European gardens, and was first observed to exhibit mutations resulting in the production of new elementary species as early as 1887, although but little doubt exists that this was by no means the beginning of its period of mutability.

#### REDISCOVERY OF *O. GRANDIFLORA* (ART.) VAIL IN AMERICA.

During the course of the investigation of the records it became evident that one or more large-flowered evening-primroses not recognized in local floras had been found in southern United States at various times. One of the most interesting of these discoveries was that of Bartram referring to a locality on the east bank of the Alabama River above Mobile and between that place and the junction of the Alabama and Tombigbee rivers. He says :

Early one morning, passing along by some old uncultivated fields, a few miles above Taensa, I was struck with surprise at the appearance of a blooming plant, gilded with the richest golden yellow; stepping on shore, I discovered it to be a new species of the *Oenothera* (*Oenothera grandiflora*, caule erecto, ramoso, piloso, 7, 8 pedalis, foliis semi-amplexi-caulibus, lanceolatis, serratodentatis, floribus magnis, fulgidis, sessilibus, capsulis cylindricis, 4 angulis,) perhaps the most pompous and brilliant herbaceous plant yet known to exist. It is an annual or biennial, rising erect seven or eight feet, branching on all sides from near the earth upwards, the lower branches extensive, and the succeeding gradually shorter to the top of the plant, forming a pyramid in figure; the leaves are of a broad lanceolate shape, dentated or deeply serrated, terminating with a slender point, and of a deep full green color; the large slender flowers that so ornament this plant, are of a splendid perfect yellow color; but when they contract again before they drop off, the underside of the petals next the calyx becomes of a reddish flesh-color, inclining to vermilion; the flowers begin to open in the evening, are fully expanded during the night, and are in their beauty next morning, but close and wither before noon. There is a daily profuse succession for many weeks, and one single plant at the same instant presents to view many hundred flowers. I have measured these flowers above five inches in diameter; they have an agreeable scent.

After leaving these splendid fields of the golden *Oenothera*, I passed by old deserted plantations and high forests, etc.

Bartram's expedition was undertaken "At the request of Dr. Fothergill, of London, to search the Floridas and the western parts of Carolina and Georgia, for the discovery of rare and useful products of nature, chiefly in the vegetable kingdom. In April, 1773, I embarked for Charleston, South Carolina, on board the brigantine, Charleston Packet, Captain Wright," etc. (Bartram, 1793, pp. 404-405.)

Seeds of the above plant were evidently sent to Fothergill, and the following is the original description of the plant by Aiton, made from specimens grown at Kew. He says "*grandiflora* 2. *Oe. foliis ovato-lanceolatis, staminibus declinatis, caule fruticoso, L' Herit.*

stirp. nov. Tom. 2. tab. 4. Great-flowered *Oenothera*, Nat. of North America. Introd. 1778 by John Fothergill, M. D. Fl. July and August" (Aiton, 1879).

It being deemed very important that a visit to the locality mentioned by Bartram should be made, Prof. S. M. Tracy, of Biloxi, Miss., generously undertook to make the search. In accordance with arrangements he proceeded up the Alabama River on August 16, 1904, and five days later came upon the plant not far from the original locality. Professor Tracy has kindly prepared the following report:

The locality for this plant, as given by Bartram, was "a few miles above Tensa." The country immediately about Tensa is mostly the dry, pine hills common in that section, and a careful search for several miles about the town did not reveal a single plant belonging to the Epilobiaceæ. Fort Mimms, 5 miles from Tensa on the bank of the Alabama River, was doubtless Bartram's headquarters while he was in that part of the State, but a careful search of the river for some miles failed of results. Dixie Landing, 25 miles above Fort Mimms by river, and 13 by road from Tensa, was the first place where the plant was seen. Immediately below the steamboat landing there is quite a stretch of abandoned fields covered with a dense growth of *Chamaecrista robusta* from 4 to 5 feet in height, and those plants are thoroughly tangled with *Bradburya virginiana*, which makes walking exceedingly difficult. The evening-primrose was found as an occasional plant in this growth, the first plants being seen about a quarter of a mile below the landing, and others being found more or less abundantly for more than a mile down the river. When growing in the thick weeds the plants were mostly erect, with simple stems, a few of which were beginning to branch at the top. A few plants were found immediately on the river bank, and even on the sides of the almost perpendicular bank, which is about 20 feet high, and when growing in that location were, as Bartram describes them, "Rising erect 7 or 8 feet, branching on all sides from near the earth upwards, the lower branches extensive, and the succeeding gradually shorter to the top of the plant, forming a pyramid in figure." The largest plant found measured 8 feet 9 inches in height. No small plants were found, and from the root and stem characters the plant is doubtless an annual. No plants were found more than 200 yards from the bank of the river, and only a few plants were found in the shade of trees. Hundreds of plants were examined, but no mature seed could be found.

A visit to Earle's Landing, 5 miles below Dixie Landing, showed the plant to be fairly abundant there also. In nearly all cases they grew on alluvial soil, which was sandy rather than heavy, and none was found near wet or marshy places. The river bank was examined nearly the whole of the distance from Dixie to Earle's Landing, and the plant was not rare on open ground covered with *Chamaecrista*, but was not seen in any other location. All of the region examined was on the east bank of the Alabama River. A gentleman owning land immediately opposite Dixie informed me that it grew in one place on the west bank.

A large number of herbarium specimens were prepared by Professor Tracy, all of which were forwarded to the New York Botanical Garden for examination, and from which seeds were obtained suitable for cultures which promise to be of great service in comparisons with the other large-flowered species of the evening-primroses.



Fig. 1. Rosette of *Onagra biennis* five months old.

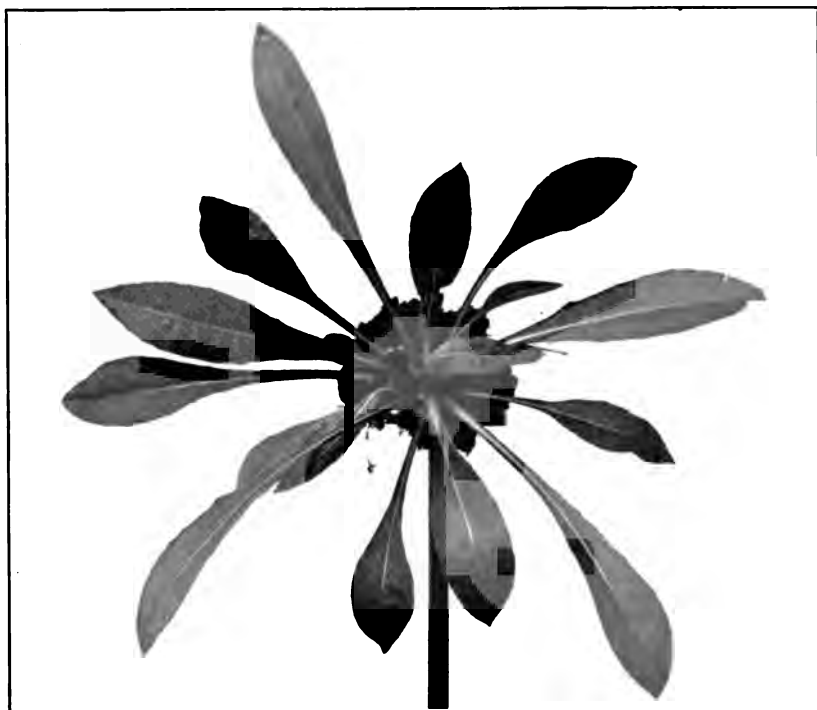


Fig. 2. Rosette of *Onagra cruciata* five months old.





## ONAGRA (OENOTHERA) BIENNIS (L.) SCOP.

Many collectors and taxonomists include a number of elementary species in *Onagra biennis* and attribute to it an extremely wide range of fluctuating variability. On the other hand, workers who have carried on cultural experiments with individuals representing a typical elementary species describe it as fluctuating between very narrow limits. The actual inclusion of the species is not so important, in connection with the present investigation, as the degree of constancy of the various strains grouped around the species and sometimes included in it.

In order to carry on observations on these points, and upon "the changes produced by cultivation," upon which some systematists lay so much stress, a number of plants of *O. biennis* (in the strictest sense), growing in uncultivated land in the New York Botanical Garden in 1903, were selected to form the basis of a pedigree-culture in 1904. Seeds were duly harvested at the end of the season and sown in the propagating house early in January. The plantlets were transferred to the experimental grounds late in May and began to bloom early in July. The species was thus grown as an annual during a season of about nine months in soil rich with fertilizers. Furthermore, the individuals were placed in rows, over a meter apart, and were kept free from the competition of weeds. Briefly stated, it may be said that in no single feature, nor in any instance, did these plants transgress the measurements, or show different forms of organs, from those of wild specimens in the vicinity. The size of the leaves, the amount of the pubescence, the size of the flowers and capsules, and the formation of the branches are capable of modification by soil-moisture, humidity, intensity of illumination, and competition, as in thousands of other well-defined species, but these modifications did not bring the species nearer in aggregate character to any of the closely allied forms. Exact records and observations were kept during the entire life-histories of the individuals, by the aid of which the following description has been prepared :

*Seedling about two months old.*—Leaves nearly glabrous ; blades oval to oblong-oval, the larger ones about 10 mm. wide, obtuse at the apex, each rather gradually narrowed into a petiole (fig. 1).

*Seedling five months old.*—Rosette open ; leaves rather copiously fine-pubescent ; blades oblong to elliptic, the larger ones fully 2.5 cm. wide, quite approximately repand-denticulate, with the teeth more pronounced at the base, acute at the apex, each narrowed into a short petiole. (Pl. III, fig. 1.)

*Mature rosette.*—Leaves ample, rather copiously fine-pubescent, the larger ones about 27 cm. long, 6 to 7 cm. wide ; blades oblong to

elliptic, or slightly broadened upwards, unevenly repand-denticulate and mostly rather jagged-toothed near the base, the petioles relatively stout.

*Adult plant* (Pls. IV and V).—Plant luxuriant, mostly 1 meter tall, or less. Stem slightly uneven, but scarcely channeled, hirsute, with spreading-ascending somewhat rigid hairs, copiously branched throughout, the lower branches decumbent, the upper ones spreading or curved upward ;\* leaves very numerous, 1.5 to 2 dm. long near the

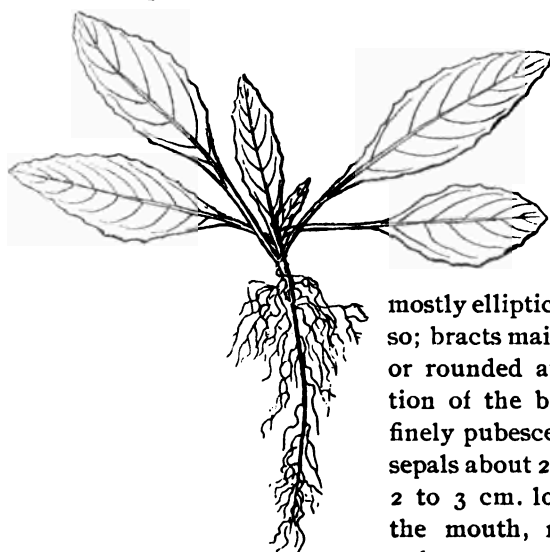


Fig. 1.—*Onagra biennis* seedling three months after germination.

base of the stem ; blades elliptic-oblancheolate to elliptic-lanceolate; shallowly but rather prominently toothed, and often jagged-toothed near the base, acuminate, those of the upper cauline leaves mostly elliptic, acute, sessile, or nearly so; bracts mainly lanceolate, narrowed or rounded at the base; conic portion of the bud 14 to 18 mm. long, finely pubescent, the free tips of the sepals about 2 mm. long; hypanthium 2 to 3 cm. long, 5 to 6 mm. wide at the mouth, nearly terete, sparingly pubescent or glabrate; sepals 15 to 20 mm. long, much shorter than the tubular portion of the hypanthium,

the free tips 4 to 5 mm. long; petals rather delicate, 12 to 16 mm. long, truncate or slightly emarginate at the apex; filaments 8 to 10 mm. long; anthers 7 to 8 mm. long; pistil shorter than the stamens; stigmas 4 to 5 mm. long; capsule 3 to 3.5 cm. long, 7 to 7.5 mm. in diameter at the thickest point, finely pubescent, slightly curved, markedly narrowed at the apex. (Pl. VI.)

It is to be seen from the above description that *O. biennis* is capable of self-fertilization by reason of the superior length of the stamens, a fact that was demonstrated in the experimental grounds. To secure purely fertilized seeds it was only necessary to inclose the inflorescence in a parchment bag during the opening of the flowers.

\*Plants growing in thickets are more spindling and have the lower branches suppressed, while the young rosettes are luxuriant, with broader leaves, under such circumstances.



*Onagra biennis*, wild specimen, grown in competition with other meadow plants.



PLATE V.



*Onagra biennis* in bloom, showing method of branching when free from competition, and growing in the open.



After an examination of material in the field in America in the summer of 1904, Professor De Vries informs the authors that the *O. biennis* used in his breeding experiments at Amsterdam differs from the foregoing, and is to be included with a form usually termed *O. biennis grandiflora* by collectors. The exact relationship of the two has not yet been carefully determined.

ONAGRA ARGILLICOLA MACKENZIE.

Within the last year a new wild species of evening-primrose has been brought to notice from the mountains of Virginia and West Virginia, being described by Mr. K. K. MacKenzie as "one of the most noticeable and common plants on the line of the Chesapeake and Ohio Railroad on both sides of the boundary line between Virginia and West Virginia." It has also been collected by Mrs. L. F. Ward, at "Alleghany," W. Va., and by Mr. and Mrs. E. S. Steele at Sweet Springs, W. Va., and the cultures in the New York Botanical Garden were begun with seeds from the latter locality. The following description has been compiled from observations on living plants of the resultant cultures:

*Seedling about two months old.*—Leaves minutely pubescent, copiously so near the base; blades oblong or elliptic-oblong, the larger ones less than 1 cm. wide, obtuse, each gradually narrowed into a copiously pubescent petiole.

*Seedling five months old.*—Rosette relatively lax; leaves minutely pubescent; blades spatulate to narrowly linear-spatulate, the larger ones over 25 cm. long, 2 to 2.5 cm. wide, repand, more distantly so and with more pronounced teeth near the base, each gradually narrowed into a long petiole.

*Mature rosette.*—Leaves numerous and conspicuously elongated; glabrous, or nearly so, except the sparingly ciliate margins, the larger ones over 40 cm. long, 2 to 2.5 cm. wide; blades broadly linear to linear-spatulate, sinuate, the teeth slightly more pronounced near the base; petioles relatively stout.

*Adult plant.*—Plant rather luxuriant, depressed in habit. Stems suppressed or very short, the branches radiate, decumbent, not channelled, somewhat tortuous, mainly 6 to 12 dm. long, puberulent and pubescent, with few spreading or ascending hairs; leaves very numerous, 10 to 15 cm. long on the lower part of the branches; blades undulate, or repand-denticulate, those on the lower part of the branches broadly linear to narrowly linear-oblong, acute or short-acuminate, each narrowed into a semi-terete petiole, those of the upper cauline leaves similar to those of the lower, but relatively shorter and broader, and



sometimes inclined to be linear-lanceolate, sessile or short-petioled; bracts lanceolate, truncate at the base, shorter than the hypanthium; conic portion of the bud about 4 cm. long, glabrous, the free tips of the sepals subulate, approximate at the base, but ascending; hypanthium 4 to 5 cm. long, about 6 mm. wide at the mouth, ridged, glabrous; sepals 34 to 47 mm. long, shorter than the tubular portion of the hypanthium, the free tips about 6 mm. long; petals rather firm, 4 to 4.5 cm. long, truncate or broadly emarginate at the apex; filaments 21 to 23 mm. long; anthers 12 to 13 mm. long; capsule 2.5 to 3 cm. long, about 7 mm. in diameter at the thickest point, glabrous, strongly curved, narrowed from the base to the apex. (Pl. VII.)

*O. argillicola* is to be distinguished by the fact that it is well adapted to securing cross-fertilization. When the flower-buds come to the morning of the day on the evening of which they will open, the pistil takes on a greatly accelerated rate of growth and pushes out of the flower-buds to a length of 3 or 4 mm., bearing the unfolded stigmas in a position in which they may readily receive pollen carried by the wind from neighboring flowers. It is not actually known, however, whether pollination is secured in this manner, or whether insects are of some aid in the matter. A similar behavior of *O. lamarckiana* near the close of the season is reported in Holland. The decumbent or non-ascendant branches of *O. argillicola* form a dense cluster which gives it a very striking appearance. The main bud of the central stem appears to remain dormant.

The great size of the flower of this species doubtless accounts for some of the reports of the presence of *O. grandiflora* in the Virginias and Pennsylvania, while the habit of the plant may have also suggested some of the notions prevalent as to the variability of *O. biennis*, with which it may have been confused.

#### ONAGRA CRUCIATA (NUTT.) SMALL.

A number of roots and some seeds of *O. cruciata* were obtained from Sandy Hill, N. Y., near Lake George, at the close of the season of 1902, and early in the spring of 1903 were divided into two portions, one of which was sent to Professor De Vries at Amsterdam, Holland. Only about a dozen plants were brought to maturity in the New York Botanical Garden during 1903, attention being directed principally to the observations on *O. lamarckiana* and its mutants.

A letter was received from Professor De Vries under date of September 19, 1903, in which he said:

Until a few weeks ago, and before flowering, the plants were a very uniform lot, with the characteristic reddish crowns and nutating tops. But now they are no longer uniform. There are two very distinct types, only differing in the

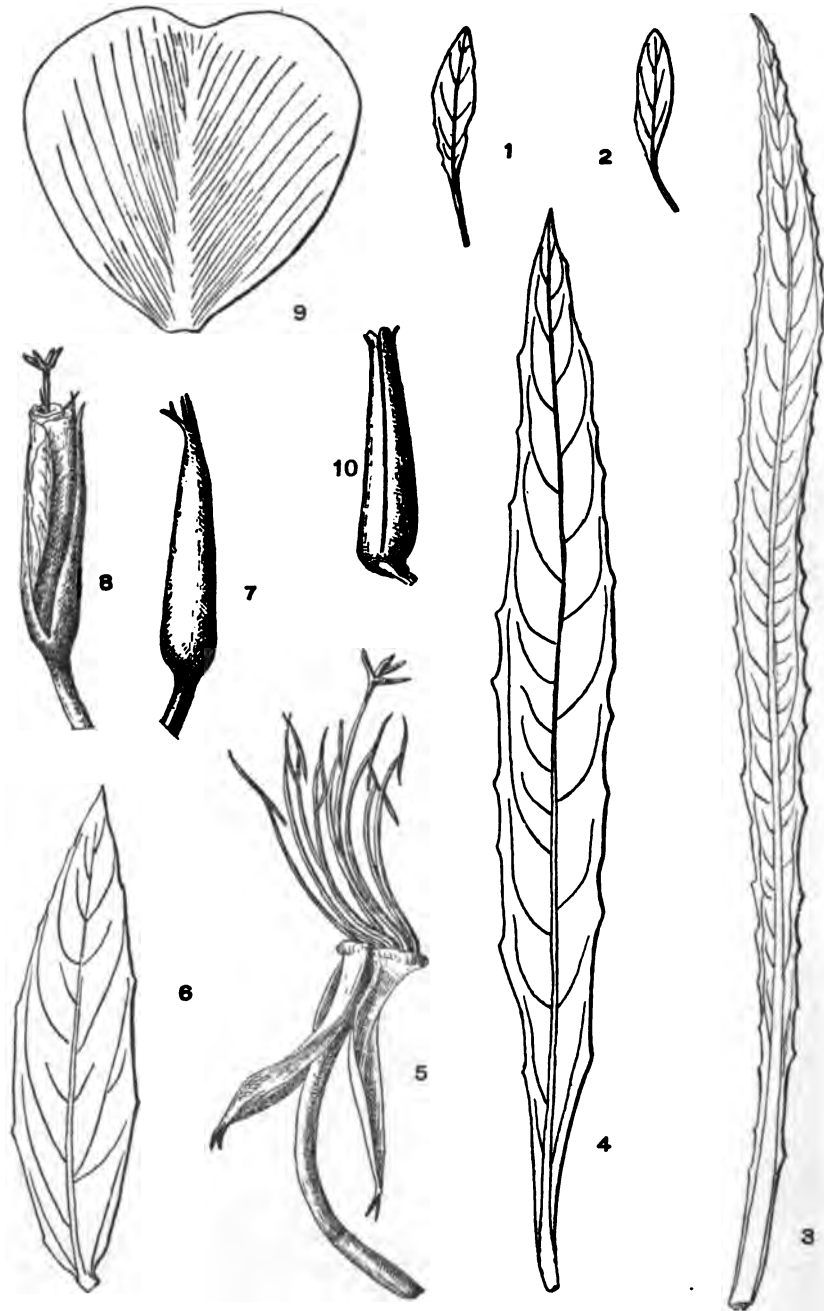
PLATE VI.



*Onagra biennis*.

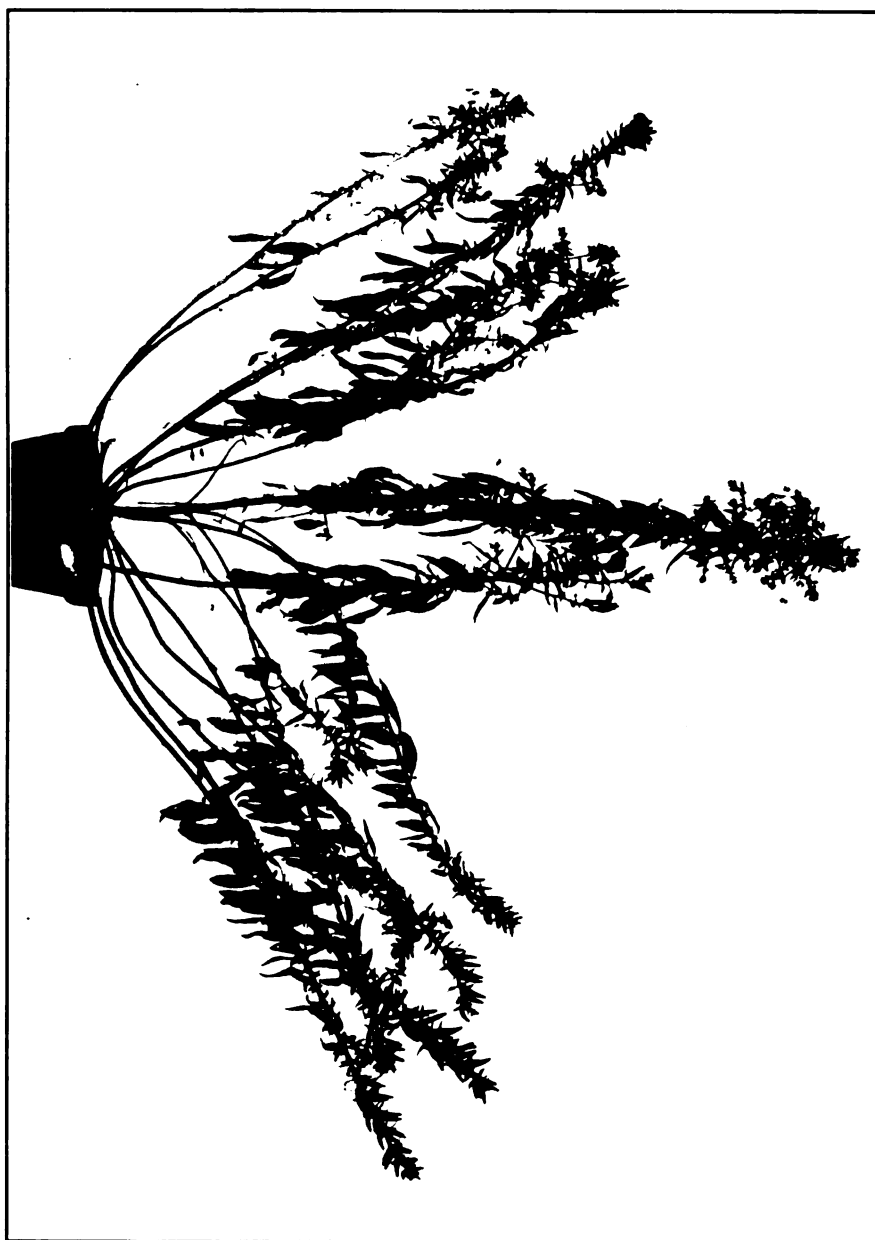
1, leaf from young rosette; 2, leaf from rosette four months old; 3, leaf from lower part of mature rosette; 4, leaf from upper part of mature rosette; 5, stem-leaf; 6, bract; 7, unopened bud; 8, flower with petals removed; 9, petals of maximum size; 10, mature capsule. 1 to 5, one-half natural size; 6 to 10, natural size.

PLATE VII.



*Onagra argillicola.*

1, 2, leaves of young rosette; 3, leaf from adult rosette; 4, stem-leaf; 5, flower with petals removed; 6, bract; 7, flower-bud; 8, flower-bud immediately previous to opening, with stigma exposed; 9, petal; 10, capsule. 1 to 4, one-half natural size; 5 to 10, natural size.



*Onagra cruciata*, showing capsule, buds, and slender hypanthium, photographed in 1903.



flowers and flower-buds. Both types are to be found in the plants coming from the seeds, as well as in those grown from the roots you sent me. The differences are slight, but striking, absolutely individual, and without transitions. Most of the individuals have broader linear petals and comparatively more rounded flower-buds. The others have narrower and therefore more strictly linear petals, and thicker buds.

I have also sown seed I got from Prof. B. L. Robinson, of Harvard University, gathered at Jeffrey, N. H., under the name of *O. cruciata*. They are wholly different from yours, being more slender, less nutating, and with a strikingly longer calyx-tube.

The same facts are given in "Species and Varieties: Their Origin by Mutation" (De Vries, 1905, p. 589), in which it is also stated that "It seems not improbable that *O. cruciata* includes a group of lesser unities, and might soon prove to comprise a swarm of elementary species, while the original strain might even now be in a condition of mutability."

The cultures of 1904 included over sixty specimens of *O. cruciata* which reached the adult stage, and included not only the two forms which he had observed to arise from the seeds and roots sent him from this place, but also the third obtained only from material from New Hampshire. It is obvious, therefore, that one form arises spontaneously from one of the other two forms suddenly, and dried specimens from the crop of 1903 in the New York Botanical Garden show that it originated in this manner here in the first year of cultivation, although the second half of the same lot of seeds sent to Professor De Vries failed to give rise to it in Amsterdam.

The evidence at hand therefore seems to confirm the suggestion as to the mutability of the species, but nothing may be said as to which of the types constitutes the parent. The characters of the forms are as follows:

*No. 1* (Pl. VIII).—Adult plant robust and luxuriant. Stem 1 to 1.5 meters tall, copiously branched, the branches spreading, sparingly hirsute, the hairs rather ascending, 1.5 to 2.5 dm. long on the lower part of the stem; blades narrowly spatulate, finely toothed near the apex, coarsely and somewhat doubly toothed below the middle, each narrowed into a short semi-terete petiole, those of the upper cauline leaves oblong-lanceolate to lanceolate, sessile, all more or less pubescent about the veins beneath; bracts oblong-lanceolate, about one-half as long as the hypanthium, truncate at the base; conic portion of the buds slender, 16 mm. long, or somewhat longer, sparingly pubescent, the free tips of the sepals 4.5 to 5 mm. long; hypanthium slender terete or nearly so, 30 or 32 mm. long, becoming glabrous, about 4 mm wide at the mouth; sepals 17 to 20 mm. long, linear-lanceolate, about

one-half as long as the tubular portion of the hypanthium, the free tips 4 mm. long; petals delicate, linear or nearly so, 10 to 15 mm. long, obtuse; filament 9 to 10 mm. long; anthers about 5 mm. long; style shorter than the stamens; stigmas about 4 mm. long; capsules 2 to 2.5 cm. long, 6 to 7 mm. in diameter at the thickest point, nearly glabrous, mainly longer than the bracts. (Pl. IX, fig. 1.)

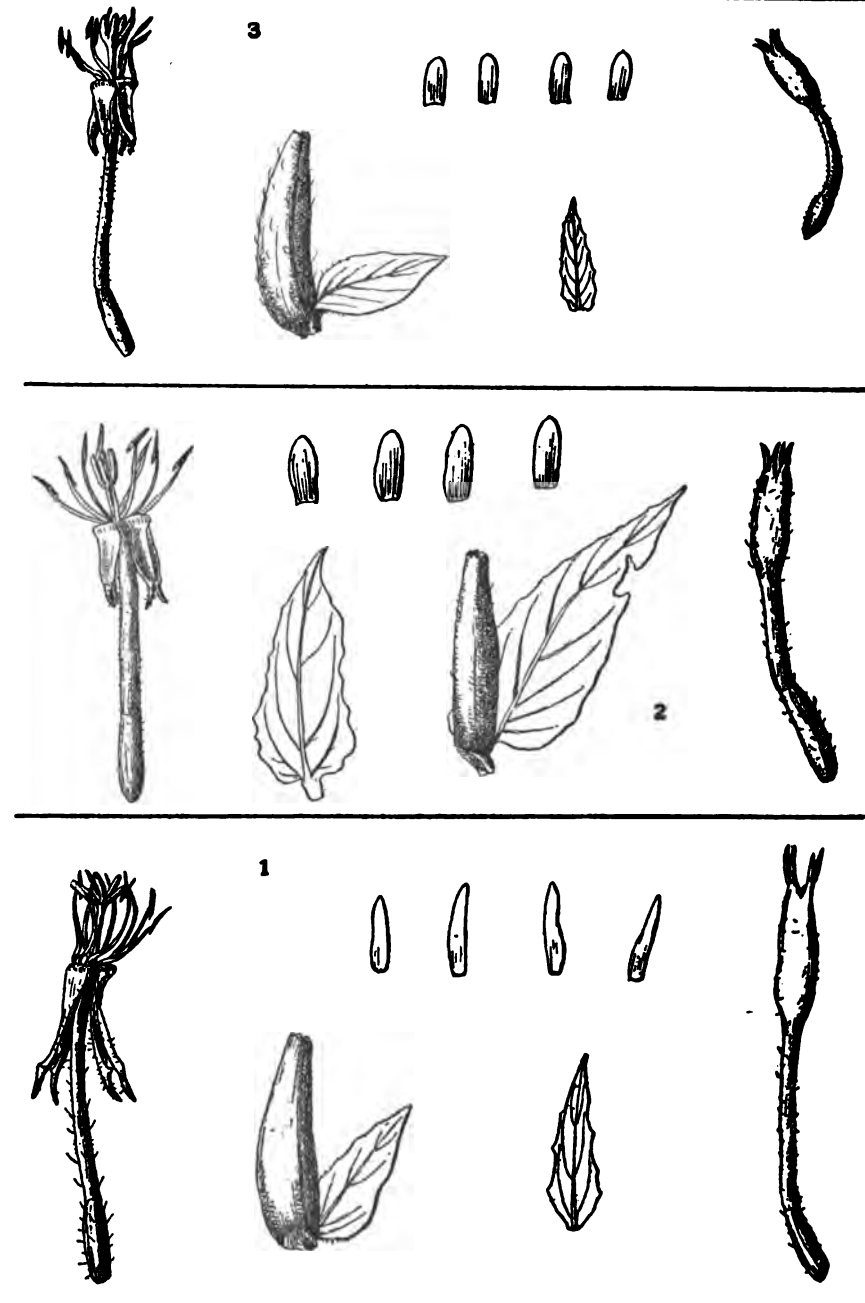
This form included about 52 of the individuals grown during 1904. The other two forms may be characterized as follows:

*No. 2.*—Bracts broadly lanceolate or ovate-lanceolate, round-truncate at the base, about as long as the hypanthium; conic portion of the bud sparingly pubescent, 15 mm. long or less; hypanthium stoutish, nearly terete, 28 to 30 mm. long, sparingly pubescent, abruptly dilated at the top, and about 5 mm. wide at the mouth; sepals 14 to 15 mm. long, linear-lanceolate, about one-half as long as the tubular portion of the hypanthium, the free tips about 5 mm. long; petals firm, broadly linear or linear-oblong, 8.5 to 10 mm. long, obtuse; filaments 8 to 9 mm. long; anthers 6 mm. long; style shorter than the stamens; stigmas 6 mm. long; capsules 2.5 to 3 cm. long, 7 to 8 mm. in diameter at the thickest point, with few scattered hairs, slightly curved, narrowed to the apex. (Pl. IX, fig. 2.) Seven individuals of this type were found in the cultures.

*No. 3.*—Bracts oblong or ovate-oblong, narrowed at the base, shorter than the ovary or slightly longer; conic portion of the buds stout, 9 to 11 mm. long, with few scattered short hairs; hypanthium slightly ribbed, stoutish, 25 to 27 mm. long, becoming glabrous, rather gradually dilated at the top and about 4 mm. wide at the mouth; sepals 9 to 10 mm. long, much less than one-half as long as the tubular portion of the hypanthium, the free tips 3 to 3.5 mm. long; petals broadly linear-oblong, 6 or 7 mm. long, obtuse; filaments 6 mm. long; anthers 4 mm. long; style shorter than the stamens; stigmas 3 mm. long; capsules about 2.5 cm. long, 7 to 8 mm. in diameter at the thickest point, with few scattered hairs, slightly curved, narrowed to the apex. (Pl. IX, fig. 3.) Six individuals were seen, all of which completed their seasonal development much earlier than the other two forms.

In the observations made during the earlier part of the development of the plants nothing was recorded by which the three forms might be distinguished, and hence the following characters may be taken to apply to the entire lot, although it is probable that most of the descriptions were made from mutant individuals.

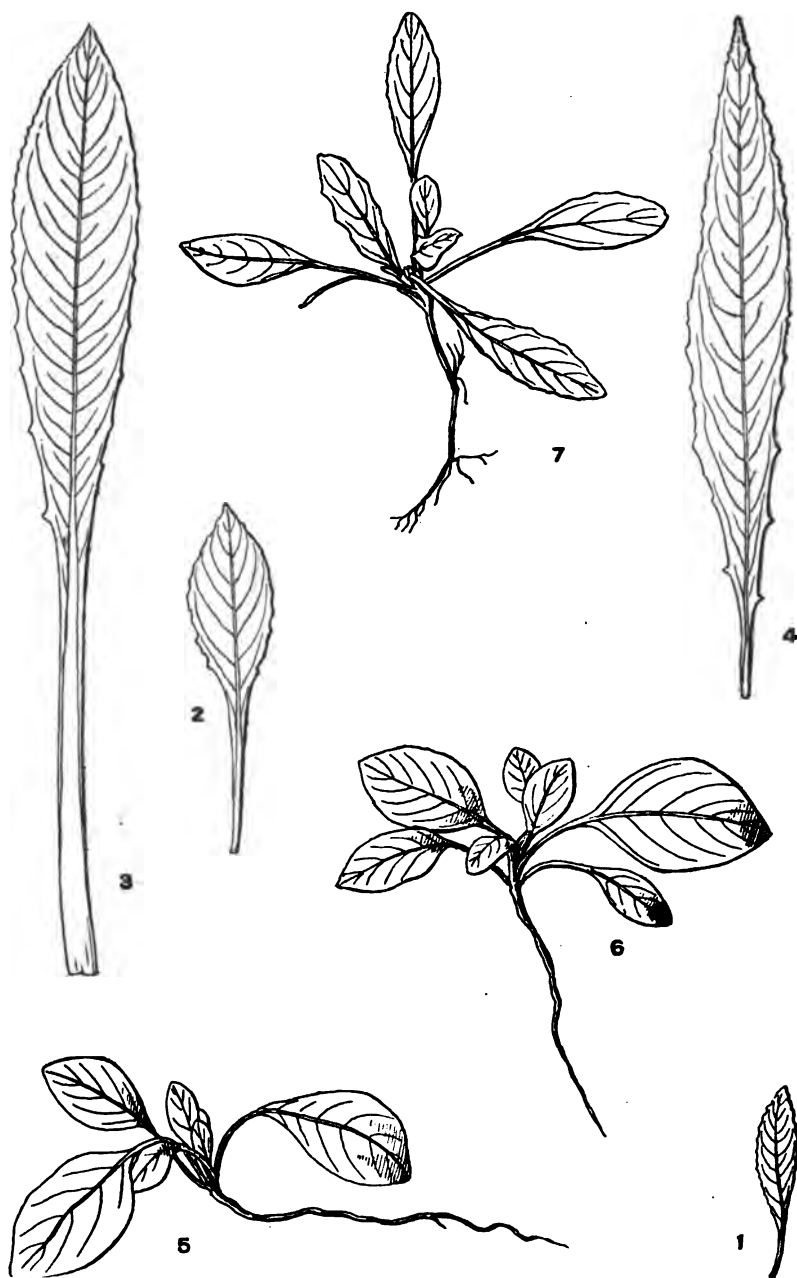
*Seedling about two months old.*—Leaves very sparingly pubescent; blades oblong, elliptic or oval, the larger ones 8 to 11 mm. wide,



*Onagra cruciata*: Buds, bracts, capsules, flowers, and petals of the three elementary forms. Natural size.



PLATE X.



*Onagra cruciata.*

1, leaf from young rosette; 2, leaf from lower part of mature rosette; 3, leaf from upper part of mature rosette; 4, stem-leaf; 5, rosette five months old; 6, rosette two months old; 7, rosette nearly five months old, with narrower leaves. 1 to 4, half natural size; 5 to 7, natural size.

undulate, obtuse or merely acutish at the apex, each rather gradually narrowed into a petiole. (Pl. X, fig. 6.)

*Seedlings five months old.*—Rosettes not dense; leaves glabrous or nearly so, except the ciliate margins; blades spatulate, some of them narrowly so, the larger ones 2 to 2.5 cm. wide, shallowly repand-denticulate, mostly acute, as long as the petioles or longer. (Pl. III, fig. 2.)

*Mature rosette.*—Leaves conspicuously elongated, obscurely fine-pubescent, the larger ones about 26 cm. long, 25 to 30 mm. wide; blades narrowly spatulate, repand-dentate, more distantly so and with prominent teeth near the base, petioles relatively slender.

All of the forms included in, and arising from, *O. cruciata* are capable of self-fertilization when the inflorescences are inclosed in bags. So far as present information goes the species of the evening-primroses native to northeastern America may be said to have comparatively small flowers and to be capable of self-fertilization, although visited frequently by flying insects. The species ranging to the southward have larger flowers, and by reason of the superior length of the pistils are adapted to cross-fertilization, although it is not definitely known that self-fertilization does not ensue. In *O. argillicola* the early protrusion of the stigmatic surfaces from the unopened flower-bud has the appearance of a positive adaptation for securing pollen from other flowers, by the agency of wind, gravity, or insects.

#### HYBRIDS.

Among the crosses made in the New York Botanical Garden during 1903, that of *O. lamarckiana*  $\times$  *O. cruciata* and the reciprocal were attempted. The first only was successful, as the castration of the flowers of *O. cruciata* was not accomplished sufficiently early to prevent self-fertilization. Likewise the removal of the stamens of *O. lamarckiana* was not done in such manner as to exclude the action of its own pollen and the pistil-parent appeared as a pure strain in the cultures.

*O. lamarckiana*  $\times$  *O. cruciata*.—A detailed study of the hybrids obtained by the pollination of *O. lamarckiana* by *O. cruciata* was made by De Vries, but the pollen-parent was evidently a highly variable hybrid race which bore the general vegetative characters of the true *cruciata*, but which showed a fluctuating variability in its flowers, from an atavistic obcordate form of petal to others of the slender *cruciata* type. The form in question is known in Europe as *Oenothera cruciata varia* and is held by De Vries to be probably a hybrid of *O. muricata* and *cruciata*. (De Vries, 1903, pp. 100-110, 593-633.)

The individuals of the hybrid as made in the New York Botanical Garden in 1903 were seen to be furnished with narrower leaves in the earliest stage of the seedlings, all of which but one were destroyed by insects before the main axis was formed. The plant was recognizable at some distance throughout its entire existence by its light yellowish-green color. The leaves of the young rosettes were ovate-lanceolate, obscurely and remotely repand-denticulate, blunt at the apex, with the laminae extending down the petioles to the bases in the form of wings 1 to 2 mm. in width. (Plate XII.)

The leaves of the mature rosette were narrowly lanceolate-oblong, being broadest above the middle and tapering to both ends, with the petioles winged. The laminae were approximately denticulate in the apical portion and irregularly so in the basal half. All of the leaves of the rosette and stem were minutely pubescent.

The stem attained a height of about 55 cm. and bore a number of short, spreading branches arising from the base of the main stem and reaching half of its length. Numerous shorter branches arose from the entire stem from a short distance above the base. The apical portions of all branches were tinged with red. The stem leaves were narrowly oblong-lanceolate, tapering to both ends and acute at both ends; 9 to 11 cm. long, and 14 to 17 mm. wide. The terminal rosettes were dense, close, symmetrical, and spreading. The first flower was shown on August 12, about six weeks later than the beginning of the blooming of either parent.

The petals were recurved after the manner of *O. cruciata* and were from 9 to 11 mm. long, varying from linear-oblong to irregularly obcordate or truncate, being entire, obscurely emarginate or irregularly notched near the apex. Furthermore, these various forms might be illustrated in a single flower (see Plate XII, figs. 6a, 7a, and 8). The definite tips of the calyx-segments were spreading in the bud and were 3 to 15 mm. long. The stamens varied in length, being shorter than the pistils in some flowers, and longer in others. The ovaries were about 9 mm. long, slightly hirsute, and the hypanthium was glabrous. The bracts were lanceolate-acuminate. The calyx-segments were much shorter than the hypanthium. The hypanthium showed a purplish tinge and the petals were flesh-color, except at the tips. The capsules were rounded, obscurely angled, 20 mm. long and 4 to 5 mm. in thickness, tapering from near the base to the tip, and bearing a few spreading hairs. (Pl. X.)

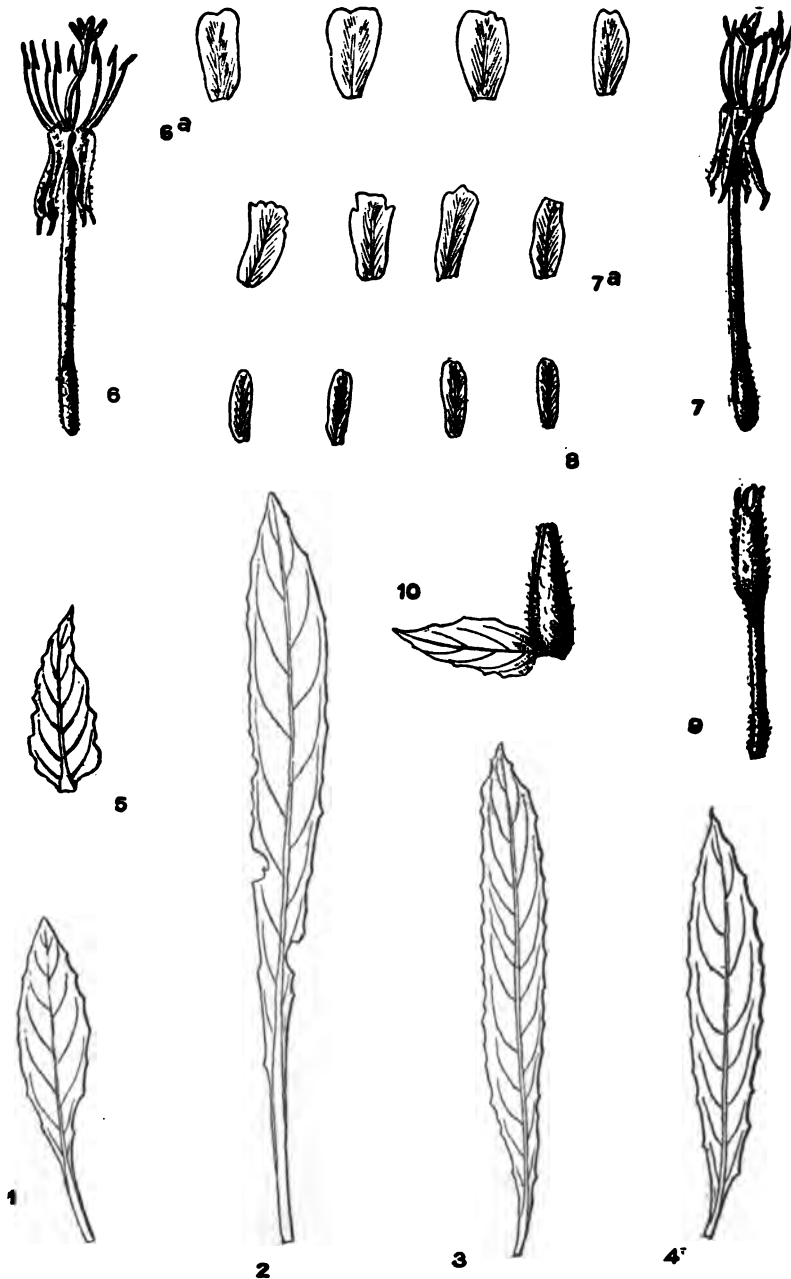
This hybrid agrees quite well with *O. cruciata varia* as described by De Vries, which he thought was a hybrid between *muricata* and *cruciata*. Whether it is actually identical with this form can not be



Adult specimen of the hybrid *Onagra lamarckiana* × *Onagra cruciata* (No. 3.21).



PLATE XII.



*Onagra lamarckiana* × *Onagra cruciata* (No. 3.21).

1, leaf from young rosette; 2, leaf from median portion of mature rosette; 3, leaf from upper portion of mature rosette; 4, stem-leaf; 5, bract; 6, flower with petals removed (see 6a); 7, flower with petals removed (see 7a); 8, petals of minimum size; 9, unopened flower-bud; 10, capsule 1 to 4, one-half natural size; 5 to 10, natural size.



definitely stated, since no living material of the latter has been examined. The only characters of the hybrid clearly derived from the pistil-parent are the relative length of the main axis and the general habit of branching. It is to be said on the other hand that the *cruciata* characters to which the general aspect of the plant is largely due are without exception more or less modified. The relative length of the stamens and pistils was seen to vary so that some of the flowers were capable of self-pollination, while in others the chance of pollination without the aid of external agencies was extremely small, so that it might be said that in some branches of the plant the *lamarckiana* character was dominant, while in others the *cruciata* self-fertilizing capacity was shown. A similar range of partial variability will be described in one of the hybrid races of the *O. lamarckiana*  $\times$  *O. biennis*.

*O. lamarckiana*  $\times$  *O. biennis*.—The results of the crosses made in the New York Botanical Garden were much more diversified than those made by De Vries, who obtained what he designates as a typical unilateral hybrid as a result of fertilization of *O. lamarckiana* by *O. biennis grandiflora*. He says (De Vries, 1903, p. 31):

The hybrid of *Oenothera biennis* (*O. biennis grandiflora*) and *O. lamarckiana* resembles the first so strongly that they can hardly be distinguished from one another. I have made this cross partly in 1894 and partly in the summer of 1899, and in the last-named year partly with *O. lamarckiana* from my own cultures, and partly from the same species grown from purchased seeds. In all cases I used *O. lamarckiana* as the mother. The stamens were taken from flowers of plants in the open (from unopened buds), and from plants of my own cultures in the last-named period. The bastards were of a single type, and were interchangeable with *O. biennis* (*O. biennis grandiflora*), not only in the rosettes, but also in the flowers and ripe fruit. I had about 50 flowering plants in 1895, and about 70 + 60 in the two series in 1899, making altogether about 180 specimens in bloom in addition to some with young stems and rosettes only (biennials). Some differences were seen, but they were not so marked or so important that a description could be made of them.

I harvested some seeds in 1895, which were secured by artificial pollination, and the second generation was grown from these in the summer of 1896. These repeated, in the 50 specimens coming into bloom, only the characteristics of the first-named parent (*biennis*).

Similarly the pollination of *O. lamarckiana* by *O. muricata* resulted in a monotypic unilateral hybrid which approximated the pollen-parent.

Four distinct types were distinguishable in the hybrid in New York, and the different forms could be recognized in a very early stage of the seedlings. All of the individuals were easily seen to be grouped around the types mentioned, and no intermediate or intergrading forms were found. The number of individuals brought to



maturity was comparatively small, and the possibility is not excluded that a culture of several hundred plants might include still other forms. In fact, the very differences between the results of the hybridizations, as carried out in Amsterdam and New York, suggest that the manner in which the various qualities in the two parents are grouped in the progeny might be capable of a wide range of variation. Many indications lead to the suggestion that the dominancy and prevalency, latency, and recessivity of any character may be more or less influenced by the conditions attendant upon the hybridization; the operative factors might include individual qualities as well as external conditions.

In addition to the hybrid individuals several specimens of the pistil-parent, *lamarckiana*, and one of its mutants appeared in the cultures, indicating that self-fertilization was not entirely prevented. This might be accounted for in two ways. Castration might not have been performed early enough to prevent the action of pollen being scattered from a bursting anther upon a mature stigma while the operation was being performed. Then, again, the possibility was not wholly excluded that pollen from the bursting anthers which fell upon the bracts inclosed in the parchment bags might have been carried to the stigmas by currents of air caused by the compression or expansion of the parchment bags. At any rate, the appearance of individuals of the pistil-parent type may be taken as presumptive evidence that such self-pollination occurred by some method, although the appearance of individuals of the parental type in hybrids is well known.

(I) A type represented by individual No. 2.1 (Pl. XIII, fig. 1) showed a rosette of deeply dull-green leaves, more or less crinkled and irregular in form and margin. In all about twelve plants of this type were seen, although but five reached a stage sufficiently advanced to send up a central stem. The rosettes were sparse and the leaves thick and fleshy, and almost glabrous, except that some were minutely pubescent on the veins beneath. The leaves of the rosettes varied from narrowly linear in the earlier stages to linear-lanceolate with obtuse apices, and to oblong-spatulate, broadest above the middle, and acutish in some individuals. The laminae were revolute and irregularly denticulate and formed narrow wings nearly to the base of the petioles.

The main axis of the hybrid individuals reached a height of 15 or 20 cm., at which stage in the development elongation ceased and the lateral branches became very active; in some instances no noticeable elongation of the main axis occurred. Branches of this were more rounded in outline and bore leaves of a structure somewhat more

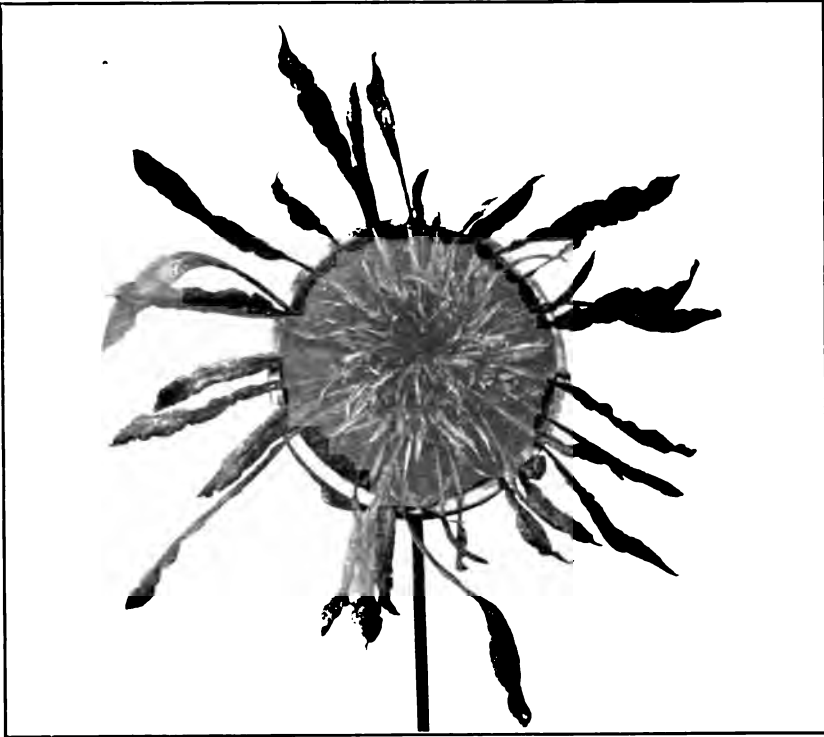


Fig. 1. Rosette five months old of No. 2.1 of the hybrid *Onagra lamarckiana* × *Onagra biennis*.



Fig. 2. Rosette five months old of No. 2.27 of the hybrid *Onagra lamarckiana* × *Onagra biennis*.



nearly conforming to normal types in a manner comparable to that of the parent, as noted above. These leaves were ovate-denticulate, abruptly acute, slightly crinkled, and were minutely pubescent. The terminal rosettes were dense and symmetrical and flower-buds were developed, the first of which opened on August 12. About this time some large rosettes were formed from lateral buds near the bases of the stems, which were composed of oblong-lanceolate leaves, slightly crinkled and denticulate and tapering to both ends. The entire plant was tinged with red, and most deeply so in the upper branches. (Pl. XVII, fig. 4.)

The petals were deeply emarginate, 28 to 30 mm. long and 30 to 35 mm. wide, being broader than long in all instances. The segments of the calyx were 30 mm. in length, being less than half the length of the hypanthium, which measured about 38 mm. The ovary was 10 mm. long and, with the hypanthium, bore a number of scattered hairs. Perhaps the most noticeable feature of this type was the variability of the relative length of the stamens and pistils. The pistils were fairly constant in length, but in some flowers the stamens were shorter and therefore not adapted to self-fertilization, while in others the anthers were above the stigmas, thus insuring self-pollination. No correlated structures were observed.

The capsules were about 2 cm. long, 5 to 6 mm. wide below the middle, oblong, tapering from near the base, obscurely angled and channeled, sparingly pubescent with both long and short scattered hairs.

The exceptional forms of leaves exhibited by this type were found to be accompanied and probably caused by the presence of a fungus, which seemed to attack this type only of the hybrid progeny. Similar effects in *O. lamarckiana* have not yet come under observation, but young rosettes of *O. biennis*, together with mature plants coming into bloom, were found growing wild in some waste park-land near the New York Botanical Garden on August 21, 1904. The leaves of these plants were closely similar to those of the pathological hybrid individual in general appearance, and furnished the curious parallel of showing a partial return to the normal form near the upper ends of the branches. Rosettes of the type described were transplanted to pots in the experimental house and the terminal portions of the leaves cut away in accordance with garden practice. Within a few days several leaves were seen to show an abundance of yellowish spermagonia, which appeared to belong to *Aecidium peckii* De Toni, although aecidia were not found.

(II) A second type was represented by individual No. 2.27, in which the leaves of the rosettes were finely pubescent on July 1; the rosettes were widely spreading and the leaves finely pubescent in specimens examined on that day. The laminae were lanceolate-oblong acute at the apex and broadest above the middle, gradually narrowing to the broad petiole and decurrent upon it to its base; approximately denticulate, crinkled between the secondary veins, more or less spotted with reddish areas. (Pl. XIII, fig. 2.)

Stems were sent up, which, upon examination on July 13, showed leaves of a dark bluish-green tinge, the laminae becoming convex upwardly owing to the unequal growth of the midrib. The stems were dotted with the reddish bases of the hairs. The apices of the main stem and of its branches formed close and symmetrical rosettes, in approximation of the structures shown by *lamarckiana*.

The general habit of the shoot was much like that of *biennis*, the basal branches being long. The central stem, however, was irregularly compressed and was of a zigzag form.

The flowers exhibited the following characters: Corolla-segments 2.2 cm. long, 2.5 to 3 cm. broad; calyx-segments 2.7 cm. long, more than half the length of the hypanthium; hypanthium 3.5 cm. long, slightly pubescent with scattered spreading hairs; ovary 6 mm. long, also pubescent with scattered spreading hairs; anthers and stigma as long as corolla, included, stigma variously 4 to 6 lobed. Bracts nearly as long as the hypanthium.

Capsules about 13 mm. long, with greatest diameter 6 to 7 mm., the greatest length being about twice the thickness; ovoid-oblong, tapering in upper portion to obtuse apex; not angled; slightly channeled; sparingly pubescent with appressed hairs. (Pl. XV, fig. 2.)

(III) The third type of the hybrid was represented by individual No. 2.24, in which the rosette was easily recognizable in the early stages and was dense, with the leaves lying flat on the ground when examined on July 1. The leaves were finely pubescent, with broadly ovate laminae, the laminae more or less crinkled, acutish or obtuse at the apex, broadest in the middle, more or less abruptly narrowed into the broadly margined petiole, which is narrowly winged at the base. These organs were approximately denticulate toward the apex, and irregularly dentate at the base, with reddish petioles and the laminae sparingly spotted with red. (Pl. XIV, fig. 1.)

The basal branches were nearly as long as the main axis. A portion of the stem immediately above the base was devoid of branches. The upper part of the stem bore numerous erect branches. The stems were deeply channeled and of a reddish color in the lower portions,



Fig. 1. Rosette five months old of No. 2.24 of the hybrid  
*Onagra lamarckiana* × *Onagra biennis*.

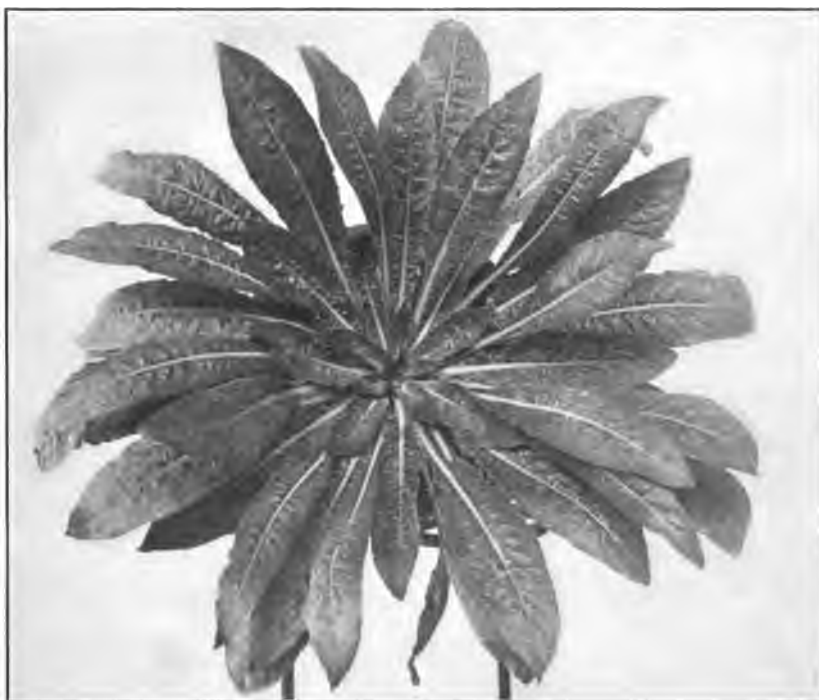


Fig. 2. Rosette five months old of No. 2.32 of the hybrid  
*Onagra lamarckiana* × *Onagra biennis*.





Fig. 1. Adult plant of 2.1 of the hybrid *Onagra lamarckiana*  $\times$  *Onagra biennis*, showing basal rosette, pathological leaves, normal leaves on upper part of stem, buds, and flowers.



Fig. 2. *Onagra lamarckiana*  $\times$  *Onagra biennis* No. 2.24 at left, No. 2.27 at right.





being distinctly paler in the terminal parts, which were of a yellowish-green color. All of the stems and branches were terminated by tufted rosettes. The following characters were exhibited by the flowers (Pl. XVII, fig. 5):

Petals 27 to 31 mm. long and 27 to 33 mm. wide, deeply emarginate; calyx-segments 30 mm. long, being more than half the length of the hypanthium, which was 48 mm. in length, slender, and glabrous, except for a few scattering hairs; ovary 12 mm. long, glabrous, except for a few scattered hairs; stamens nearly as long as the pistil. The capsules were 29 to 32 mm. long, 6 to 7 mm. in thickness, being about four times as long as broad, distinctly four-angled, and shallowly channeled; oblong and narrowed in the apical region; sparingly appressed pubescent. This type was noted as producing perfect seeds in apparently smaller numbers than the other types of the hybrid, although some branches bore several well-filled capsules. (Pl. XV, fig. 2.)

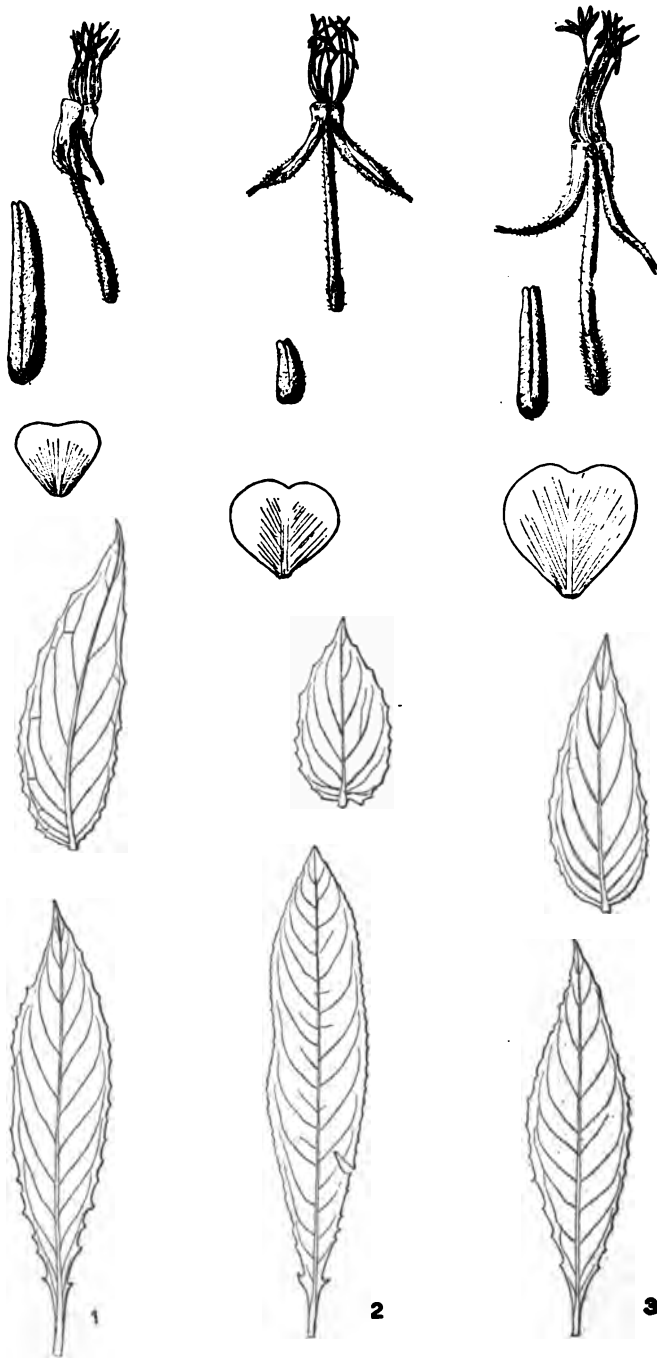
(IV) A fourth type was represented by individual No. 2.32, which was not recognized in the rosette stage, although the leaves are much narrower than in *O. biennis*, and are not so deeply toothed in the basal portion. The aspect of the adult plant (Pl. XIV, fig. 2) is very marked, however, and it is easily recognizable. The lateral branches are numerous and nearly as long as the main axis, with the stems deeply channeled. The larger leaves of the rosette are narrowly oblong-lanceolate and yellowish-green, with prominent reddish midveins. The stem leaves are lanceolate and broadest about the middle and deeply toothed. The entire plant is pubescent and shows a tinge of reddish color even when young, which becomes much intensified with age. (Pl. XIV, fig. 2.)

The bracts are oblong-ovate, the hypanthium longer than its segments; the petals are about 20 mm. long and 24 mm. wide, with wedge-shaped bases. The stamens, pistil and petals are about of the same length. The green capsules are about 26 to 27 mm. long and 6 to 7 mm. thick, oblong, tapering from near the base to the narrow apex, and shining green, being only sparingly pubescent. The general outline of the capsules is irregular; in cross-section they appear distinctly four-angled. (Pl. XVI, fig. 3.)

Seven individuals of this type were brought to maturity and all conformed, with only minor divergences, to the above structures.

The hybrid progeny in the cultures made in the New York Botanical Garden and in Amsterdam was thus seen to include a series of types which ranged, in the aggregate of characters included, from those

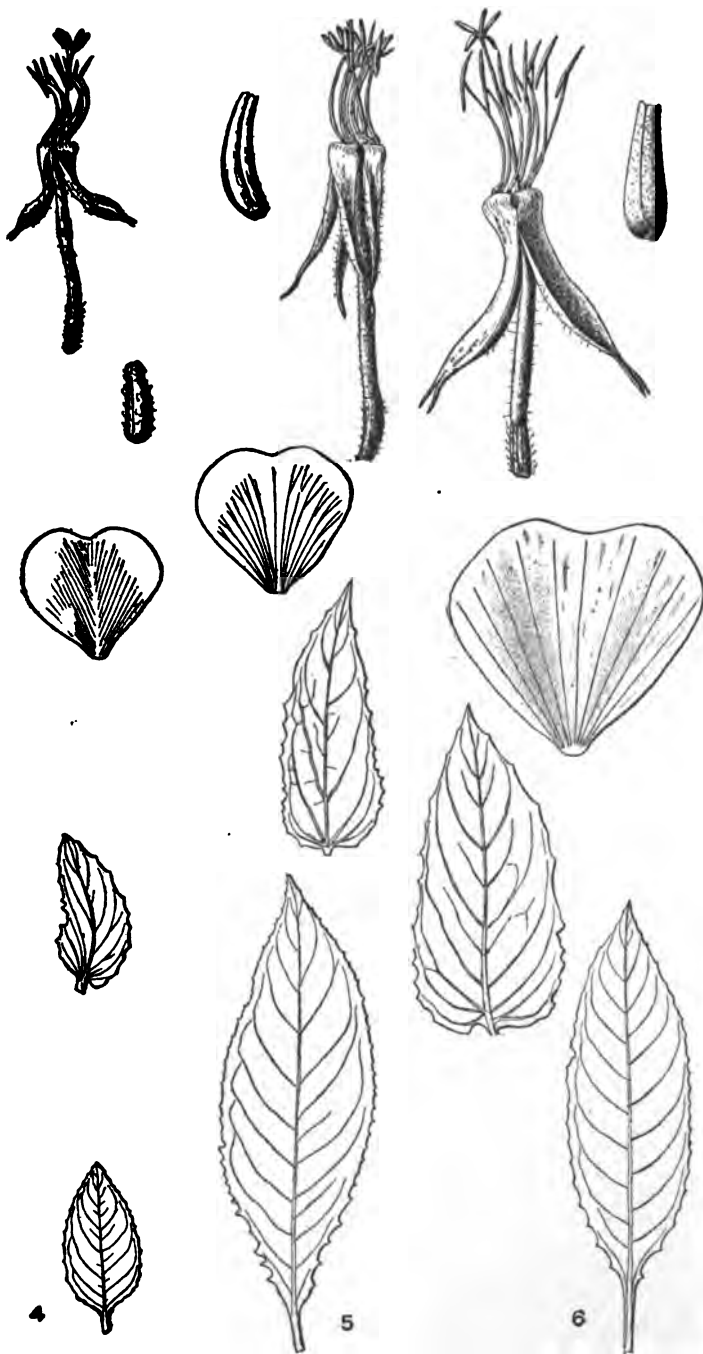
PLATE XVI.



Stem leaves, bracts, petals, capsules, and flowers of *Onagra biennis* and of two of the four hybrid types of *Onagra lamarckiana*  $\times$  *Onagra biennis*.

1, *Onagra biennis*; 2, No. 2-27; 3, No. 2-32. Stem-leaves one-fourth natural size; remainder of figures five-eighths natural size.

PLATE XVII.



Stem-leaves, bracts, petals, capsules, and flowers of *Onagra lamarckiana*, and of two of the four hybrid types of *Onagra lamarckiana*  $\times$  *Onagra biennis*.

4, No. 2-1; 5, No. 2-24; 6, *Onagra lamarckiana*. Stem-leaves one-fourth natural size; remainder of figures five-eighths natural size.

representing pure strains of both parents through goneoclinic forms to intermediates in which the parental characters were more or less equally apparent.

Although the great difficulties attendant upon a valuation of the characters occurring in hybrids were appreciated, it was concluded that such an estimation expressed in tabulated form would be the best method of expression of the dominance of the various characters.

Hurst selected twenty anatomical characters which were assigned equal value, and included such features as the habit of growth, and form and shape of the leaves and other organs, and upon the prevalence of these characters the degree of relationship of the hybrid to the parent was estimated. (Hurst, 1900.)

Peter made a tabulated list of the external characters of the hybrids of the hawkweed, in which these characters were classed as unilateral, goneoclinic, or intermediate with respect to the corresponding features of the two parents. The dominance of any given character was calculated from its occurrence in the entire list of plants examined. (Peter, 1884.)

Mathematical expressions of the dominancy of qualities are in themselves misleading unless based upon actual physical measurements taken by statistical methods from a number of individuals to eliminate errors. Then, again, the estimation of the development of a paired character presents one of the greatest difficulties encountered in the study of hybrids. Authors are by no means agreed as to what constitutes absolute dominance. Until within the last few years a character was regarded as dominant by most writers only when it appeared in the hybrid as an exact reproduction of the parental quality. The most recent discussion upon this subject that has come to notice is that of Correns, who takes the ground that a character apparently representing the parental quality to 75 per cent of its full power may be considered as dominant, when occurring to the extent of 25 to 75 per cent as intermediate, and below 25 per cent as recessive. (Correns, 1903.)

This author calls attention to the fact that fully dominant characters occur but rarely, and cites examples of *Hyoscyamus* and *Bryonia*.

The comparatively small number of individuals (33) of the hybrid between *O. lamarckiana* and *O. biennis* which were brought to maturity did not give extended opportunities for statistical work, and the number of characters taken into account included many not susceptible of direct physical measurement. It was decided, therefore, to express the descriptions in taxonomic terms arranged in tabulated form to serve as a graphic illustration of the general complexion of

the types embraced by the hybrid. In this scheme it was found most convenient to apply the terminology generally used to designate the aspect of an individual to that of the separate characters, and qualities which were fully dominant and accurate representations of the parental forms were placed under the heading of "unilateral;" those which approximated the type of one parent closely, but did not represent it sufficiently to be identical with it in ordinary descriptive work, were classed as "goneoclinic" to that type, while those in which an average of the paired characters was apparent were placed under "intermediate." It is evident that the "intermediate" of Correns would embrace both the "intermediate" of the above classification and the goneoclinic departure from it on either hand. Goneoclinism may well be the extreme of fluctuating variability instead of a modification of a group-quality. The scheme used below has been found most convenient for this special discussion, but it is not urged as the best method for the general estimation of hybrids.

*Tabulated analysis of the characters occurring in the various types of the hybrid  
Onagra lamarkiana × Onagra biennis.*

No. 2.1.

	Unilateral.	Goneoclinic.	Intermediate.	Goneoclinic.	Unilateral.
	To lamarkiana.			To biennis.	
Rosettes .....					Leaves dull-green, fleshy, narrow, with irregular outlines, affected by parasite.
Stems and leaves.	Leaves crinkled. Terminal rosettes symmetrical.	Upper leaves ovate, denticulate.			Lower leaves thick, waxy, affected by parasite.
Flowers and fruits.		Capsules tapering to near apex, short, and thick.	Relative length of stamens and pistils variable.		Calyx-segments shorter than hypanthium.

The notable feature of the structure of this type consists of the forms of leaves exhibited by the stem. The rosettes and leaves of the stem which are attacked by the fungus are almost exact counterparts of those of *O. biennis*, while the upper portions of the shoot bear foliage-organs, very similar to those of *O. lamarkiana*. The tendency to being attacked by the fungus seemed confined wholly to this type, which is entirely unlike the remainder of the progeny in characters not affected by the parasite.

Tabulated analysis of the characters occurring in the various types of the hybrid  
*Onagra lamarckiana* × *Onagra biennis*—Continued.

No. 232.

	Unilateral.	Goneoclinic.	Intermediate.	Goneoclinic.	Unilateral.
	To lamarckiana.			To biennis.	
Rosettes .....	Leaves crinkled.	.....	Leaves erected.	.....	Leaves narrow, not deeply toothed.
Stems and leaves.	Stems channelled.	.....			Leaves narrow, deeply toothed.
	Terminal rosettes symmetrical.	.....			Branches long and numerous.
Flowers and fruits.	Ovary sparingly pubescent.	.....	Capsule oblong, tapering at apex.	Capsule four-angled and tapering at apex.	Relative length of hypanthium to calyx-segments 31:41.
			Hypanthium of average length of parents. Petals wider than long.		Bracts oblong-ovate; petals wedge-shaped at base. Stamens as long as pistils; pistils as long as petals.

Entire plant becoming deeply tinged with red when mature.

No. 224.

Rosettes .....	Leaves crinkled.	Young leaves broadly ovate, acutish or obtuse at apex.	Mature rosettes dense, spreading. Leaves broad, rounded at apex.	Young leaves denticulate. Basal portion of older leaves irregularly denticulate, tapering to petiole.	.....
Stems and leaves.	Leaves crinkled, hanging down, densely arranged.	.....	Stems reddish...	Leaves ovate-lanceolate, denticulate throughout.	Basal branches as long as main axis.
	Upper branches erect, spreading.	.....	.....	.....	.....
Flowers and fruits.	Bracts subcordate, oblong-lanceolate, acutish, or acuminate.	Capsule nearly glabrous, tapering from near base, slightly channelled.	Petals intermediate in size and in relation of length and breadth.	Hypanthium thin.	Terminal rosettes tufted. Relative length of hypanthium and calyx-segments as in biennis. Relative length of stamens and pistil as in biennis. Capsule distinctly four-angled.

Among the characters noted above, all may be traced to the influence of one or other of the parents directly, except that of the excessively long and thin hypanthium. This organ sustains the proportions of some of the large-flowered relatives of *O. lamarckiana*.

*Tabulated analysis of the characters occurring in the various types of the hybrid  
Onagra lamarckiana × Onagra biennis—Continued.*

No. 2.27.

	Unilateral.	Goneoclinic.		Goneoclinic.	Unilateral.
	To lamarckiana.		Intermediate.	To biennis.	
Rosettes ....	Leaves crinkled.	Mature rosettes dense, leaves with long petioles.	.....	Young leaves oblong-lanceolate, tapering at base.	Leaves spotted with red. Leaves of mature rosettes, lanceolate-oblong.
Stems and leaves.	Leaves crinkled. Terminal rosettes dense and regular, leaves deeply green.	.....	Length of stem-leaves average of parents.	Leaves of mature rosette not so deeply and regularly denticulate as in biennis. Basal branches not as long as main axis.	.....
Flowers and fruits.	Basal portion of petals rounded.	Bracts ovate, acute, irregularly denticulate, rounded or obscurely cordate at base. Capsule ovoid.	Petals with length greater than width. Superficial extension average of parents. Capsule pubescent, obscurely channeled.	.....	Stamens and pistils of same length; capable of self-fertilization.

The stems were irregularly compressed with a zigzag outline, in a manner reminiscent of those of *O. rubrinervis*. The upper leaves of the rosettes and of the stems were strongly convex upwardly, due to the unequal growth of the laminae and midrib. The calyx-segments were relatively shorter than in either of the parents. The entire shoot of the adult plant was deeply tinged with red.

It is to be seen from the foregoing that the hybrid *O. lamarckiana* × *O. biennis* obtained from the crosses made in New York includes four distinct and separate forms, none of which are identical with the unilateral monotypic hybrid obtained in the same cross in Amsterdam. In the last-named form the qualities of the pollen-parent were fully dominant throughout, while in the four types the qualities of the two parents exhibit diversified mosaics of dominancy and latency of the parental characteristics.

One of the American types, No. 2.1 (Pl. XVII, fig. 4), was characterized by a predisposition to the attacks of a fungal parasite, *Aecidium peckii*. The portions of the plant affected exhibited structures quite similar to those of the pollen-parent when affected by the same organism. Organs not directly attacked by the fungus showed such



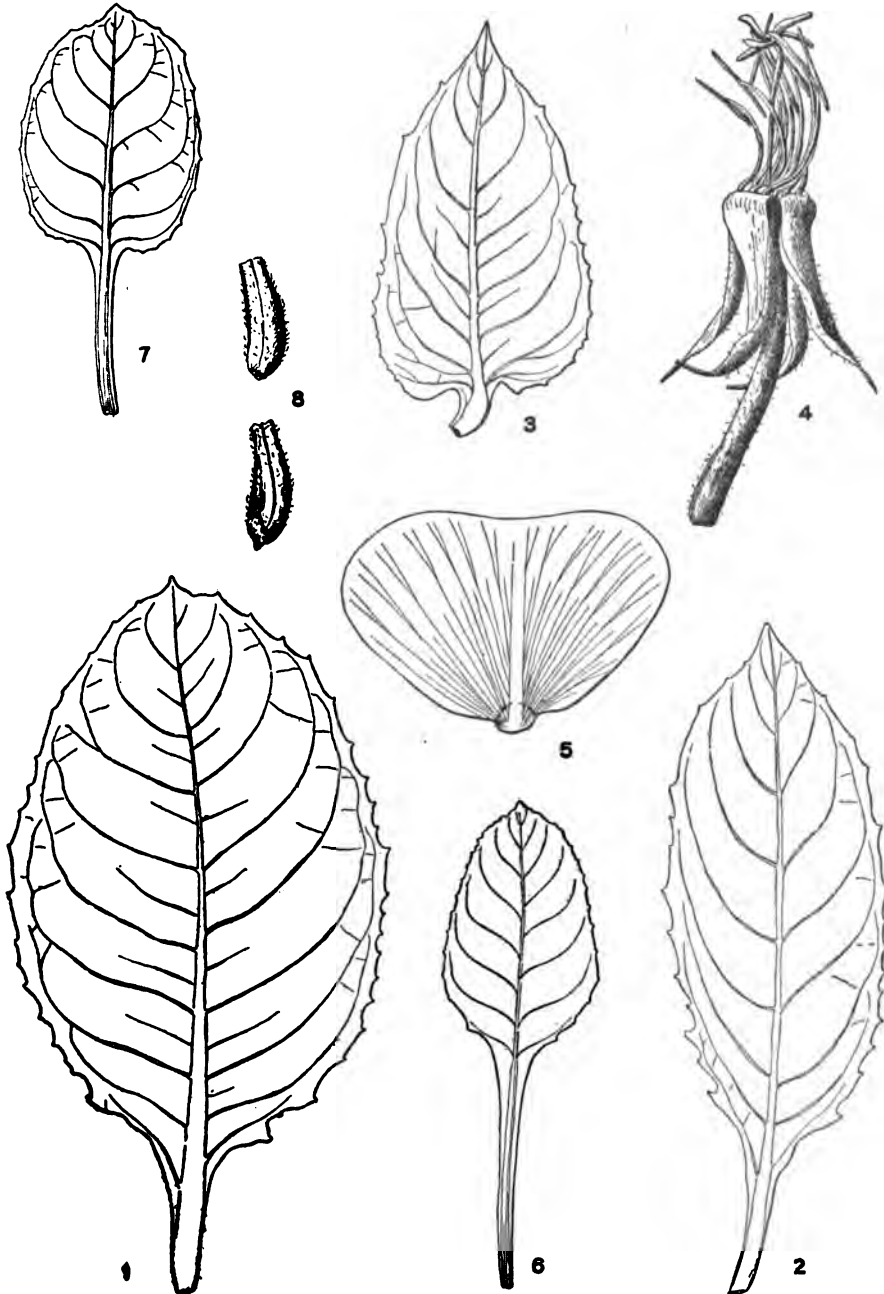
distinctive form as to make it certain that the diseased plants were not simply pathological individuals of one of the other types, but that the hybrid included a strain incapable of resisting the attacks of the fungus. The entire crop of seeds obtained by the cross in the previous year were sown in a single seed-pan, and this strain was seen to be affected even in the first foliage-leaf, while all of the others were found to be wholly immune. The whole pathological effect may be said to be due to the dominance of qualities of *biennis*. Leaves not directly attacked by fungus, on the other hand, exhibited a predominance of qualities characteristic of *O. lamarckiana*. The variable length of the stamens and pistils may, however, most reasonably be ascribed to the pathological condition.

A second form, No. 2.32 (Pl. XVI, fig. 3), reproduces the *biennis*-characters of the bracts, relative dimensions of the pistils, stamens, and petals quite exactly, and shows only slight departures from this parent in the habit of branching and form and margins of the leaves. The relative measurement of the hypanthium and of the petals are alike in the parents and remain the same in the hybrid. Only one character seems to have been transmitted unchanged from the *lamarckiana* parent, while the stems are channeled something after the manner of this parent, and some crinkling of the leaves is present. In this instance the qualities of *biennis* predominates strongly in the hybrid, and the qualities inherited from the other parent are of comparatively minor physiological importance. It is notable, however, that the general aspect of this plant is very different from that of *biennis*, although the taxonomic analysis yields so little actual anatomical divergence. This is partly due to the unusual reddish color present in the leaves and stems.

A third type, No. 2.24 (Pl. XVII, fig. 5), was characterized by the combination of parental qualities in such manner as to constitute intermediates. The characters of the form, size, and structure of the stems and leaves made a mosaic of modifications from both parents, in which it would be difficult to assign greater importance to one over the other. The hypanthium exhibited a length greater than that of either parent, while the ovary was less pubescent than either. The amount of red color present in the stems and branches was much greater than that of either parent and is only duplicated among some of the related species of the genus.

The form and structure of the bracts and the crinkling of the leaves were transmitted unchanged to the individual; the size and form of the petals were intermediate, and the relative length of the calyx-segments and hypanthium of *biennis* were found. It was notable

PLATE XVIII.



*Onagra gigas.*

1, leaf from middle of main stem; 2, leaf from main stem; 3, bract from one of the lowermost flowers; 4, flower with petals removed; 5, petal; 6, leaf from lower part of rosette five months old; 7, leaf from upper part of rosette five months old; 8, capsules. 1, 2, 3, 4, 5, and 8, five-eighths natural size; 6 and 7, one-fourth natural size.



that the spread of foliar surfaces and the density of arrangement of the leaves was similar to *lamarckiana*, while the form, incisions in the margin, and arrangement at apices of branches were similar to *biennis*. In the same manner the capsule was nearly glabrous, but was found to be distinctly four-angled.

A fourth type, No. 2.27, bore flowers not easily distinguishable from the pollen-parent, being capable of self-fertilization, but with the parts of the flower of greater size. From the other parent the unequal growth of the leaves, which results in the crinkling of the laminae is shown with a modification which causes convexities and concavities.

The symmetrical terminal rosettes are also a *lamarckiana* character of the entire laminae. An analysis of the remaining characters show that nearly all are combinations of parental qualities. Perhaps the most remarkable feature of this type is the appearance of qualities usually exhibited only by species allied to the parents and not by the parents directly. Among these may be mentioned the zigzag formation of the stem and the red coloration of the shoot.

In view of the above results it is evident that a repetition of the crosses between the mutant derivatives of *O. lamarckiana* and *O. biennis* would yield much of interest. De Vries has repeatedly called attention to the fact that the prevalency of the parental types in crosses of mutants with each other and with the parental form may be altered by nutritive conditions, and it may well be supposed that a similar state of affairs may be found to exist in the hybrid described above.

It will be of interest to trace the dominancy of the separate characters of the two parents throughout the hybrid considered as a whole. Of these the one that may be seen earliest in the development of the plantlets is the density of the rosettes due to the rapidity with which the leaves on the shortened internodes of the young stems appear, and their duration. Every individual in the hybrid, without exception, showed a heavy rosette composed of about 12 to 20 leaves, after the manner of *lamarckiana*. Plantlets of *biennis* of a similar age never bore more than half that number. The character in question depends upon the activity of the internode; the dominant character entails a more rapid succession of development in these members, as no difference could be detected in the duration of the individual leaves. While the character itself would be classed as meristic in its nature, yet it is really seen to rest upon a real and constant physiological quality. In addition to the rate of growth, it is not improbable that the greater density of the dominant rosette may be due in part to the development of a greater number of internodes before the elongated flowering shoot is sent up.

The leaves of all rosettes of the hybrid showed laminae variously crinkled, caused by the unequal growth of the mesophyllary and fibrovascular tracts of the laminae, a character which is well marked and constant in *O. lamarckiana*, but which was not seen in *O. biennis* in any of the cultures, although it has been seen in a few wild specimens which were growing luxuriantly. Furthermore, the crinkling of the leaves was exhibited in the stem-leaves of the entire hybrid. In one type, that illustrated by 2.27 and consisting of two individuals, a further lack of correlation in the growth of the tissues of the leaf was exhibited, which consisted in an excess growth of the midrib over that of the wings of the laminae, giving it an upward convexity which might easily be converted into the reverse form. This was present in both the rosette and stem-leaves.

The forms of leaves were so diversely intermediate that it is not possible to point to any important dominancies in this respect, except such as are found in the types of terminal rosettes exhibited by stems and branches. One, a regular, flattened, and symmetrical rosette, characteristic of *lamarckiana*, was dominant in all individuals except those of 2.24, which bore tufted rosettes in the five individuals included with it.

The branching habit of *O. biennis*, by which secondary members were borne on all parts of the main axis, decreasing in length upwardly, showed exactly the complementary prevalency, being present in all individuals with terminal rosettes of the pattern of *O. lamarckiana*. Type No. 2.24, which bore *biennis* rosettes, gave off large basal branches, and the upper part of the main axis was more densely branched than in *O. lamarckiana*, so that the habit of the pistil-parent in this particular was not exhibited in pure form by any member of the hybrid.

Stems of rounded cross-section were found to be more prevalent than those with deep channeling, the latter occurring on only five individuals of the hybrid.

The capacity for self-fertilization as indicated by the relative length of the stamens and pistil was dominant in all types, except that of 2.1, or in about 29 out of the 33 individuals examined. A sharp separation with regard to this character may be detected in securing pure fertilizations. In order to obtain capsules with pure seeds it is but necessary to inclose the inflorescences of *O. biennis* in the parchment bags and the pollen will fall on the stigmatic surfaces without the intervention of any agency whatever except gravity. On the other hand, *O. lamarckiana* rarely sets seeds unless pollen is transferred to the stigmas by insects or by hand, although in the open air the same purpose is sometimes accomplished by the wind.

The calyx-segments are relatively much shorter than the hypanthium in all individuals of the hybrid showing a dominance of a character of *O. biennis*, although the actual length of the latter is greater in some individuals than in either parent. The other features of the flowers were variously intermediate. The elongated capsule was present in all of the individuals of the hybrid, except in the two included in the type of No. 2.27.

#### OCCURRENCE OF MUTANTS.

Among the progeny arising from the cross between *O. lamarckiana* and *O. biennis* were two individuals which, as early as July 1, were seen to be separable by the variously erect leaves with long petioles in the rosettes. The rosettes were sparse, and the leaves were oblong-lanceolate, obtuse at the apex, broadest about the middle, and more or less abruptly narrowing to the petiole, upon which the narrow wings of the laminae extended nearly to the base. The basal portions of the leaves were deeply and irregularly denticulate. The members of the rosette were minutely pubescent. On July 13 these plants had sent up shoots which soon bore the characteristic leaves, bracts, and flowers of *O. rubrinervis*, a mutant which was originally observed by De Vries in 1887.

The occurrence of mutants in hybrids in which one of the parents appears as a pure strain has long been known and has been described at length by Professor De Vries as occurring at numerous times in his cultures. He found that about 1 per cent of the hybrid progeny of *O. lamarckiana*  $\times$  *O. nanella* was composed of mutants, and that about 2 per cent of the hybrid progeny between various older species were mutants in a series of tests made in 1896-1900. (De Vries, 1903, pp. 425, 426.)

*O. rubrinervis* was observed by De Vries to arise in the hybrid progeny of *O. lamarckiana*  $\times$  *nanella*, *O. lata*  $\times$  *nanella*, *O. lata*  $\times$  *lamarckiana*, *O. lata*  $\times$  *brevistylis*, *O. nanella*  $\times$  *brevistylis*, *O. scintillans*  $\times$  *nanella*, and *O. lamarckiana*  $\times$  *scintillans*, to which must be added the experience related above, by which this species was also found in the descendants of *O. lamarckiana*  $\times$  *biennis*.

The facts recorded by De Vries indicate that the mutability of the various forms of the evening-primrose is not modified by crossing in any manner. It is a matter of interest in this connection that he has also established the conclusion that the number and amplitude of fluctuating variations exhibited by parental forms are not increased or materially modified in the hybrids.

The designation of an individual from a hybrid progeny as a mutant is unsafe, unless, as in the evening-primroses, the characters of the mutants have been established by previous observations. It is quite possible that mutants may have appeared in hybrids at various times, thus giving basis for the assumption that new qualities were seen to appear as a result of the hybridization.

A second occurrence of *O. rubrinervis* as a possible mutant was noted in a lot of plantlets grown from seeds obtained from the botanical garden at Upsala early in 1904. The seeds were sown in germinating pans on March 28, 1904, and four individuals were transplanted to the experimental grounds on May 28 and began to send up shoots early in July. Of these, two were undoubted types of *O. rubrinervis*, corresponding to this form in all particulars.

In reply to the inquiry as to the derivation of the seed from which the above plants were grown, Prof. F. R. Kjellman, director of the botanical garden at Upsala, replied as follows under date of August 8, 1904:

The seeds of *Oenothera lamarckiana*, which you received from this botanical garden, were gathered from plants grown in a cool house from seeds obtained from Professor De Vries. Some oenotheras of other species were growing near these plants, upon which account the possibility of hybridization was not excluded. Pure seeds of the new species of *Oenothera* may, in my opinion, only be obtained from Professor De Vries.

In view of the above record, therefore, it may only be said that the specimens of *O. rubrinervis* in this culture owe their origin either to an actual mutation, or to the pollination of *O. lamarckiana* by *O. rubrinervis*. Professor Kjellman did not state whether or not any of the new species were included in the lot growing near *O. lamarckiana*, although the negative presumption seems warranted.

Still a third occurrence of the same species is to be noted, for which all explanation is lacking at the present time. A package of seeds under the label of "*Statice Japonica*" were received from the botanical garden at Tōkyō, in 1903. After germination, four of the seedlings were transplanted to small pots in accordance with the usual custom with new accessions to the New York Botanical Garden. Attention was not called to the peculiar appearance of these plants until early in May, when they formed rosettes 2 dm. in diameter, and were unmistakably *O. rubrinervis*. I was not able to trace the history of the seed-package and learn whether all of the seeds were of the same kind or not. If by mistake a package of seeds of *Onagra* had been sown under the above label, the *rubrinervis* which was with it would

have germinated first, as the seeds are very easily awakened from the dormant condition, and a half dozen of these would have been transplanted to small pots by the gardener and the remainder would have been destroyed in accordance with the usual custom. A still further possibility lies in the fact that ordinary seeds are sown in mixtures of potting soil that has not been sterilized, and might have contained some seeds of this species from the cultures made in the New York Botanical Garden for the previous year.

The chief purpose of the earlier studies of the senior author of the present paper was to make comparative studies of the parent-form with its mutant derivatives, and also to test the stability of all of the types concerned when cultivated under climatic conditions widely different from those under which the mutants arose. Previously to the cultures of 1904 less than a dozen of the various forms were brought to maturity, and no attention was given to the possible occurrence of mutants among the seedlings, although many might have been present. Thus De Vries found 600 mutants in 50,000 seedlings from *lamarckiana*, although he has pointed out that it would be possible to have extensive plantations of seedlings which included no divergent forms. Still another factor in the matter consisted in the inexperience of the experimenter. The discovery of the mutants in the seedling stage when only two or three small leaves are present is difficult for the first time, although after becoming accustomed to the typical forms and learning the aspect of the things to be looked for it is comparatively easy to recognize the better-known mutant types. Even then the mutants previously seen are much more readily distinguished than those known only by descriptions. This matter of practical observation depends greatly upon the plain mechanical fact that the selection of the various forms is generally done in the seed-pans in which germination occurred in order to save the labor necessary in transplanting them to small pots.

After the major ends of the cultures had been reached in the summer of 1904, and the newly-grown crops of seed were nearly mature, the chances of losing any of the forms under cultivation by accident was reduced to a minimum, and all of the seeds remaining on hand were sown in pans of sterilized soil in order to make separate observations upon the occurrence of mutants. Several thousands of seeds of *O. lamarckiana* of the crop of 1901 from the botanical garden of Amsterdam, and of the same species of the crop of 1903 from the New York Botanical Garden, were germinated in the above manner. In addition, a few hundred seeds of *O. gigas* of the crop of 1903 from the botanical garden of Amsterdam were sown



The seedlings of the last-named species show a wide divergence in the juvenile leaves, which is partially continued even in the foliar organs of the mature plant, although it is not believed that these divergences may be grouped in separate strains of the species. Consequently several selections were made from the cultures which, however, were soon found to be well within the limits of the type.

The results obtained from *O. lamarckiana* were of much greater interest. Mutants were found in the seedlings grown directly from the seeds from the garden at Amsterdam, and also from those of 1904 from the New York Botanical Garden. As early as October 1, 1904, *O. albida*, *O. elliptica*, and *O. scintillans* were recognizable in the plantlets grown from seeds produced in New York and Amsterdam. Later, *gigas*, *nanella*, *oblonga*, and *subovata* were found. In addition to these seven known mutants which had been seen to originate previously in Amsterdam, seven other forms could be distinguished which could not be identified with any forms heretofore observed by Professor De Vries or the authors. It is therefore justifiable to say that so far as present information goes the range of mutability of the parent-species has been extended under the conditions under which it has been cultivated in America. A comparative examination of the cultures in the two localities brings out the fact that the plants grown in New York were much more vigorous and active than those in Amsterdam, and the suggestion lies close at hand that whatever the causes may be that induce changes in the qualities of a species, the actual environment in which such mutative alterations ensue is one that has a majority of the factors favorable to vegetative development as well as to plentiful seed-production. The limited number of facts brought to light by the mutation cultures certainly support the suggestion in question, which, it is to be noted, is in direct opposition to the conclusion of Darwin that new types arise most plentifully in response to adverse circumstances.

In conjunction with the foregoing it is to be recalled that seeds of *O. lamarckiana* obtained from Vilmorin-Andrieux et Cie., in France, by De Vries, produced some *O. nanella* when sown in the botanical garden at Amsterdam in 1899. (De Vries, 1903, p. 459.)

It is to be seen, therefore, that *O. lamarckiana* is still in a mutable condition in various portions of its widely extended range. The results of the more recent cultures made in the botanical garden at Amsterdam leads, however, to the conclusion that *O. lamarckiana* has lost the capacity for producing *O. lata*, *laevifolia*, and *brevistylis*. De Vries also found that the capacity for mutability inherited by *rubri-*



Fig. 1. *Onagra lamarckiana* and *Onagra nanella* in bloom.  
Photographed at 6 a. m., August 9 1904.



Fig. 2. *Onagra lamarckiana*  $\times$  *Onagra biennis*.  
No. 2.32 at left and right in foreground; No. 2.24 in center.



*nervis*, by which it was able to give rise to *nanella*, no longer exists. The loss of mutability has been noted to be accompanied by an acquisition of the Mendelian procedure in the hybridization of these two forms. (De Vries, 1903, pp. 458, 460.)

The discovery of single plants presumably derived from an ancestral mutation, or of a few plants as mutants from a parent, suggest that in some instances the period of mutability of a species may include only a single season, and these brief periods may recur at intervals concerning which information is totally lacking. In the case of *oenotheras*, however, the first mutants in bloom were found in 1887, which shows that the parents from which they were derived perfected their seeds in 1885. The recurrence of various mutants has been noted in every succeeding year, including 1904, and it is to be seen, therefore, that this species has been in a mutable condition for twenty years. How much earlier mutants have been formed than the date given above cannot be surmised. The continuance of the capacity for mutability is open to actual observation, however, and it may be possible within the next few years for the botanist to actually witness the closing of the mutative period in this plant which has furnished material so rich in practical and theoretical results. The procedure of *O. lamarckiana* is supposed by De Vries to be similar to that which has been followed by *Draba* and *Viola* in the productions of the swarms of species now recognized. (De Vries, 1905.)

During the cultures of 1902-1903 *O. lamarckiana*, *O. nanella*, and *O. rubrinervis* were grown as biennials for purposes of comparison with the behavior of other species. During 1904, however, seeds were sown in the propagating houses about the first of the year and the plantlets, after being properly transferred from smaller to larger pots, were placed in the soil in the experimental grounds in the latter part of May. No marked difference between the two series could be detected. It was noted that *O. gigas*, however, has more thoroughly established itself in the biennial habit and that not half of the plants grown as annuals actually produced flowers or seeds in 1904.

The estimation of the general hardiness or fitness of the parental form and of the mutants, with a view to the determination of their relative value if thrown into a competitive struggle for existence, is not to be too lightly made. *O. lamarckiana* has not spread over any part of North America having the climate of New York, and its cultivation in this locality must bring into contact many factors inoperative in its natural habitat. Tests made under such conditions must be accepted most guardedly. A general description of some of the more striking characteristics of the various forms will be of some value, however.

The rosettes of *O. lamarckiana* and *O. rubrinervis* which failed to send up flowering shoots in 1903 endured the following winter, which was of maximum severity, and began growth in a normal manner in the spring of 1904, but were uprooted to make room for a new series of experiments.

No actual difference has been found in the power of producing pollen among the parent-form, the mutants grown in the New York Botanical Garden, and the other American species. All produce an abundant crop of pollen, and show many faulty grains. *O. rubrinervis* was found to produce a greater number of capsules, and the seeds germinated more readily than those of the parent-form, the plants reaching maturity earlier than *O. lamarckiana*. *O. gigas*, on the other hand, grows more slowly than the parent-form, as stated above, although it



FIG. 2. Seedlings of *Onagra gigas*, about five weeks old, showing variations in forms of leaves.

produces seeds abundantly, which show a high percentage of germination. Both species are supposed by De Vries to be quite equal to the parental type in vigor, or perhaps to excel it. The latter suggestion is supported by the marked reproductive capacity of these forms in hybridizations. When crossed with the parental form or with other mutants, the dominance of the characters of *O. gigas* and *O. rubrinervis* is especially marked, most so in the case of *O. gigas*.

In continuation of the work carried on in previous cultures observations of *O. gigas* were made for the purpose of placing on record an exact description of its characteristics as grown in America. The formal descriptions of the parental type and *O. rubrinervis* and *O. nanella* have already proved useful in the various phases of the present investigation. (MacDougal, 1903.)



Fig. 1. *Onagra gigas* in bloom.  
Photographed at 7 a. m., August 9, 1904.

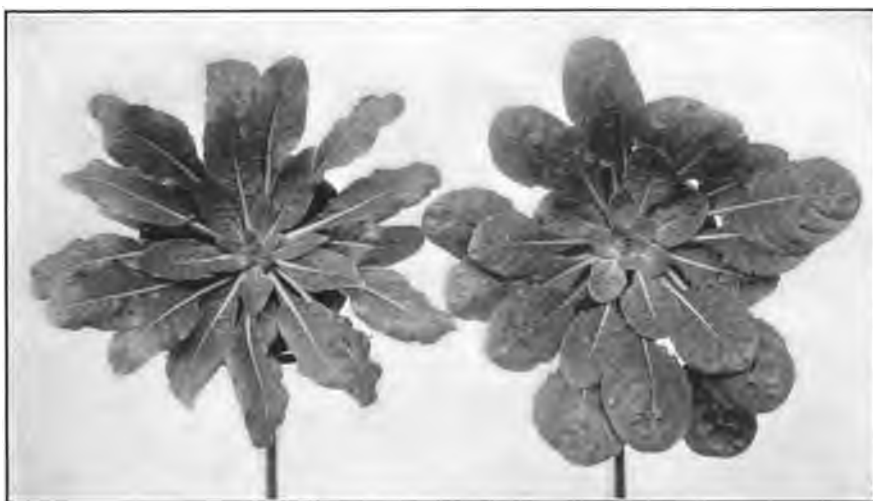


Fig. 2. Rosettes of *Onagra gigas* six months old, showing diverse forms of leaves.



PLATE XXI.



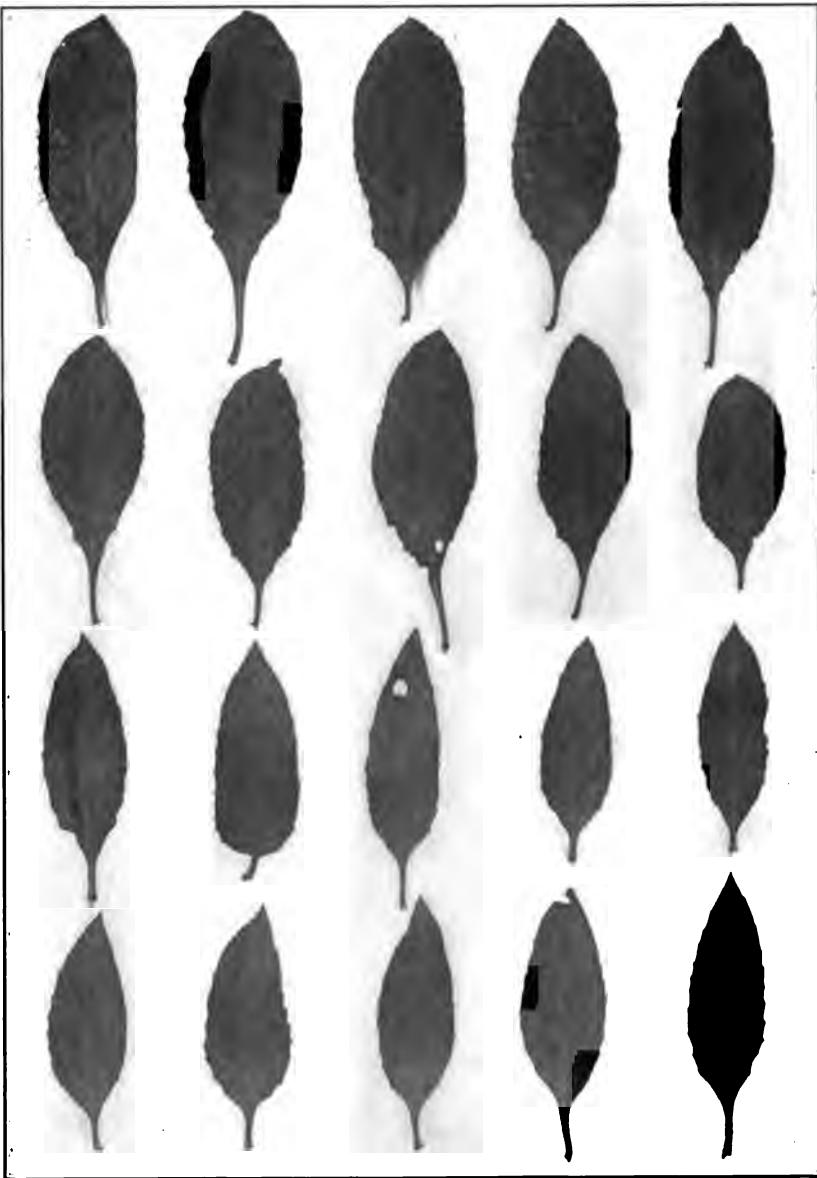
*Onagra rubrinervis.*

Photographed at 6.30 a. m., August 9, 1904.





PLATE XXII.



A series of leaves taken from near the middle of the basal branches of *Onagra lamarckiana* and *Onagra rubrinervis*, illustrating the nearest approach to identity in leaf-form. The two lower rows are *Onagra rubrinervis*; the two upper *Onagra lamarckiana*.



## ONAGRA (OENOTHERA) GIGAS.

*Seedling about two months old.*—Leaves finely but rather copiously pubescent; blades various; those of the earlier leaves narrowly or broadly oblong, those of the later leaves broadly oval, suborbicular, or ovate-orbicular, mainly 3 to 4 cm. wide, abruptly narrowed at the base, or truncate, longer than the petiole.

*Seedling five months old.*—Rosettes rather dense; leaves copiously fine-pubescent; blades broadly oblong, oval, or ovate, varying to obovate, the larger ones 2.5 cm. wide, distantly denticulate, obtuse or nearly acutish at apex, markedly longer than petiole. (Pl. XX, fig. 2.)

*Mature rosette.*—Leaves ample, finely pubescent all over, the larger ones about 28 cm. long, 9 to 10 cm. wide; blades ovate and prominently glandular-denticulate, or with an ovate terminal lobe and several large basal teeth, or tooth-like lobes, with petioles very stout.

*Adult plant.*—Plant very stout and luxuriant. Stem channeled, branched near the base, and mainly below the middle, the branches assurgent or ascending, like the main stem hirsute, the hairs commonly widely spreading; leaves finely pubescent, 1 to 2 dm. long, on the lower part of the stem, numerous; blades shallowly and rather remotely toothed, those of the lower cauline leaves oblong-spatulate to oblong, acute at the apex, each narrowed into a semi-terete, margined petiole, those of the upper leaves broadly oblong to oblong-ovate, acute or abruptly short-acuminate, sessile or nearly so; bracts ovate-lanceolate, cordate or subcordate at the base; conic portion of the bud about 3.5 cm. long, finely pubescent, with short, spreading hairs, the free tips of the sepals 6 to 7 mm. long; hypanthium 4 to 4.5 cm. long, about 7 mm. wide at the mouth, slightly ribbed; sepals 4 to 4.5 cm. long, about as long as the tubular portion of the hypanthium, the free tips 8 to 9 mm. long; petals firm, 4.5 to 5 cm. long, truncate or slightly emarginate at the apex; filaments 18 to 20 mm. long; anthers 15 to 16 mm. long; pistil longer than the stamen; stigma 6 to 7 mm. long; capsule about 2 mm. long, 7 to 8 mm. in diameter at thickest point, finely pubescent all over, scarcely narrowed at apex. (Pl. XVIII.)

### STATISTICAL COMPARISONS OF *ONAGRA* (*OENOTHERA*) *LAMARCKIANA* WITH TWO OF ITS MUTANTS.\*

So general is the experience in garden practice that a variety which has been improved by selection rapidly loses its improved character upon the cessation of the selective process that the stability of any modification which is discovered either in nature or under cultivation demands the fullest possible proof. The mutation-theory is so diametrically opposed to Galton's law of ancestral heredity that it needs especial investigation from the same standpoint and by the same methods by which this law was established. According to Galton's law the offspring shows a certain definite degree of inheritance from each generation of its ancestors, one-half from its parents, one-quarter from its grandparents, one-eighth from its great-grandparents, and so on. (Galton, 1889.) As a consequence of this law the children of extreme parents are on the average less extreme than their parents, because their preparental ancestry is on the average more mediocre. The departure of the offspring from the mean condition of the race to which it belongs toward the extreme condition of its parents has been designated "regression." One of the most serious criticisms which has been made upon De Vries's conclusions has been that of Weldon, who points out that no satisfactory evidence has been presented to prove the completeness of regression, in the Galtonian sense, in the *Onagra* mutants. For, unless such regression is complete, these mutants could not maintain themselves distinct from the parental type except through the agency of man in guarding pollination and in selection, a fact which would deprive them of all significance in the explanation of evolution. (Weldon, 1902.)

To test quantitatively the continuity or discontinuity of a few of the differential characters of the *Onagra* mutants, and to begin the work which, when continued for several years, will forever set at rest the question of the completeness of Galtonian regression, the investigation the results of which are reported in this section were undertaken. The number of specimens available for study was not sufficient for the most satisfactory statistical work, but the results offer a number of suggestive lines for future investigation.

As all the characters chosen for this investigation are notably affected by the physical conditions to which the plants are subjected, it should be pointed out that all these specimens were grown near each other in an experimental garden which presents nearly uniform conditions throughout, and that they were planted at the uniform

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\*Prepared by G. H. Shull.

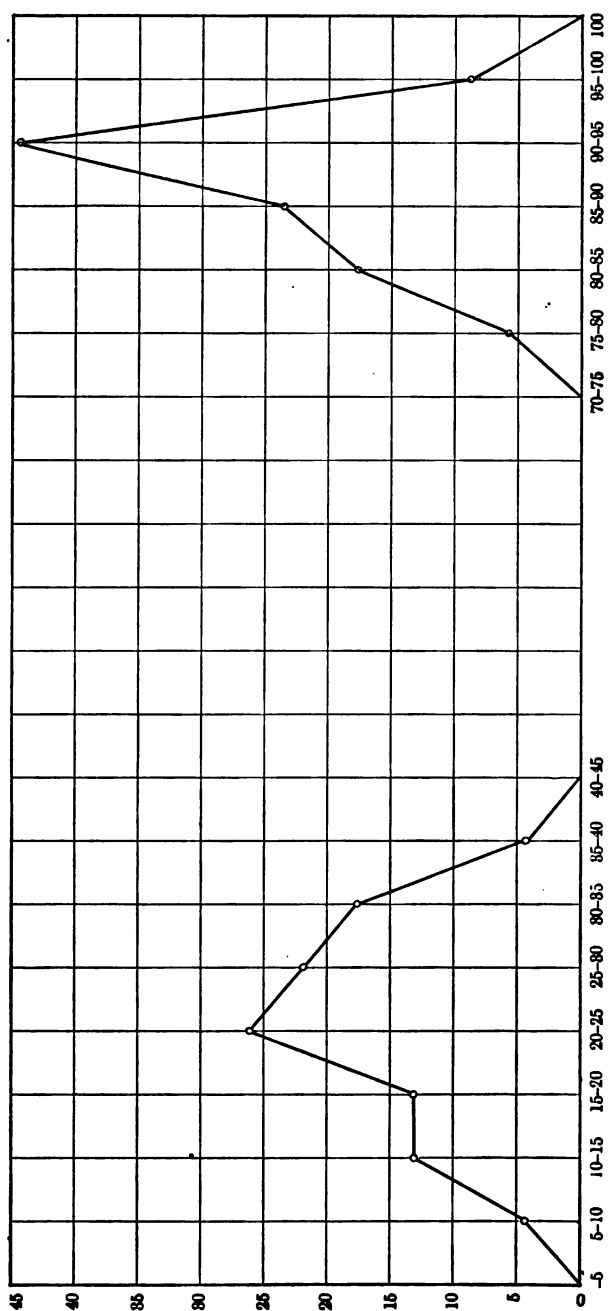


FIG. 8. Variations in stature of *Onagra nanella* (left) and *O. lamareckiana* (right). *O. nanella*: Range, 7-35 cm.; M.,  $22.81 \pm 1.02$  cm.;  $\sigma$ ,  $7.26 \pm 0.72$  cm.; C. V.,  $81.84 \pm 8.16$  per cent. *O. lamareckiana*: Range, 77-96 cm.; M.,  $88.68 \pm 0.56$  cm.;  $\sigma$ ,  $4.76 \pm 0.39$  cm.; C. V.,  $6.37 \pm 0.44$  per cent.

distance from each other of one meter, thus allowing each specimen sufficient space to express its characteristic physiological nature unmodified by complex interrelations with other plants.

*The stature of Onagra nanella.*—The character which most strikingly differentiates *O. nanella* from its parent-form, *O. lamarckiana*, is that from which it has so appropriately received its name. The great difference in height between these two species may be seen in the photograph (Pl. XIX, fig. 1), which represents a typical specimen of each. The results of measuring 23 specimens of *O. nanella* and 34 of *O. lamarckiana* are seriated in the form of curves of equal area in fig. 3. It will be observed in this figure that not only are the two curves quite distinct, but that they are separated by a wide gap. The discontinuity is tremendously in excess of the probable errors, the distance between the means of the two curves being more than forty times the sum of the probable errors of the means. The heights of *Onagra nanella* group themselves about the mean value  $22.81 \pm 1.02$  cm., with a range from 7 cm. to 35 cm., and those of *O. lamarckiana* about the mean value  $88.68 \pm 0.55$  cm., with a range from 77 cm. to 96 cm. The other constants present quite as interesting differences. Although the mean height of *O. nanella* is only one-fourth as great as that of *O. lamarckiana*, the standard deviation,  $\sigma$ , is considerably greater, being  $7.26 \pm 0.72$  cm. in the former and only  $4.76 \pm 0.39$  cm. in the latter. As the mean and the standard deviation are combined in the formula  $\frac{100\sigma}{M}$ , to form the coefficient of variability, the latter

constant shows an even more remarkable difference between these two forms than do the means. The coefficient of variability in the height of *Onagra nanella* is notably high,  $31.84 \pm 3.16$  per cent., while that in *O. lamarckiana* is quite as notably low,  $5.37 \pm 0.44$  per cent. This is particularly interesting, as will be seen later, in its agreement with the fact that in most of the characters chosen for this study the mutant is significantly more variable than the parent-form.

*The branching habit of Onagra rubrinervis.*—The nature of the branching of *O. rubrinervis* as compared with that of *O. lamarckiana* is such as to give it a very characteristic aspect. On the average about twice as many of the axillary buds develop branches and these branches have a greater average length. In both species there is a whorl of long lateral branches surrounding the base of the main axis. In *O. rubrinervis* the central axis bears numerous branches roughly correlated with their position on the axis in such a way as to give the plant as a whole a distinctly conical form. In *O. lamarckiana*, on the other hand, the branches arising from the central axis are less numer-

ous, shorter, and evidently less closely correlated with their position on the axis, but show a tendency to group themselves somewhat above the base, so that the plant resembles the framework of an inverted umbrella. (Cf. Pl. XIX, fig. 1, and Pl. XXI.)

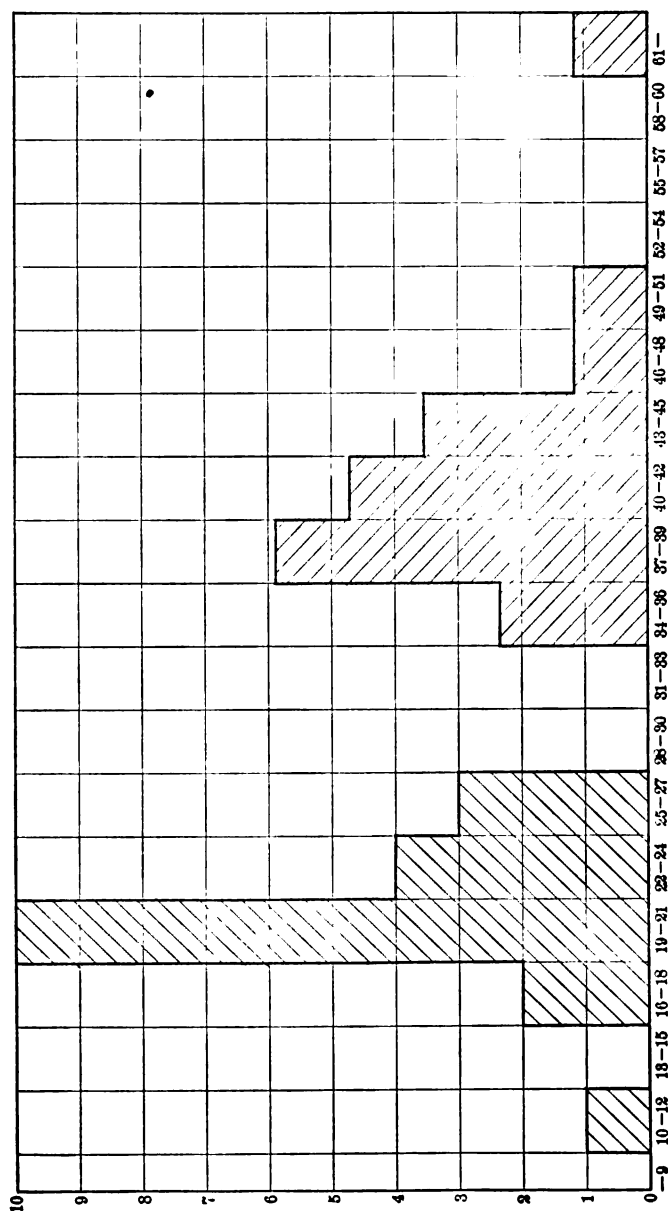


FIG. 4. Variation in number of lateral branches in *Onagra lamarekiana* and *O. rubrinervis*. Curve for *O. rubrinervis* shaded with lines rising to left. *O. lamarekiana*: Range, 11 to 25; M., 20.70  $\pm$  0.49;  $\sigma$ , 8.24  $\pm$  0.85; C. V., 16.7  $\pm$  1.7 per cent. *O. rubrinervis*: Range, 84 to 62; M., 42.85  $\pm$  1.04;  $\sigma$ , 6.84  $\pm$  0.78; C. V., 15.0  $\pm$  1.7 per cent.



Although such a character as this is too largely influenced by the individual physiological vigor to be of any value as a diagnostic character, the difference of aspect between the lots of plants of these two species was so striking that it was thought interesting to give it quantitative expression. A comparison of the number of lateral branches shows complete discontinuity between the two species in this regard, the range in *O. lamarckiana* being from 11 to 25, and in *O. rubrinervis* from 34 to 62. Curves of equal area representing the variation in the number of branches of 17 specimens of *O. rubrinervis* and of 20 specimens of *O. lamarckiana* selected by lot, are shown in fig. 4. The constants of these curves are as follows:

	Mean.	Standard deviation.	Coefficient of variability.
	<i>Meters.</i>	<i>Meters.</i>	<i>Per cent.</i>
<i>Onagra lamarckiana</i> .....	20.70 $\pm$ 0.49	3.24 $\pm$ 0.35	15.7 $\pm$ 1.7
<i>Onagra rubrinervis</i> .....	42.35 $\pm$ 1.04	6.34 $\pm$ 0.73	15.0 $\pm$ 1.7

If, instead of the number of branches, we consider the total branch-length, the results are in some respects more striking still, for in general the branches are longer in *O. rubrinervis* than in *O. lamarckiana*. This did not prove invariably true, however, and the discontinuity which should have been increased by this difference in average length is lost through the occurrence of a specimen of *O. rubrinervis* having a total branch-length of only 7.79 meters, though it had 39 branches. This is well within the range of total branch-length of *O. lamarckiana*, which varied in this respect between 3.65 meters and 8.41 meters. The greatest length of branches observed in any specimen of *O. rubrinervis* was 29.98 meters. The variability in regard to total branch length is presented graphically in fig. 5. The constants of these curves are as follows:

	Mean.	Standard deviation.	Coefficient of variability.
	<i>Meters.</i>	<i>Meters.</i>	<i>Per cent.</i>
<i>Onagra lamarckiana</i> .....	6.68 $\pm$ 0.20	1.35 $\pm$ 0.14	20.2 $\pm$ 2.2
<i>Onagra rubrinervis</i> .....	18.19 $\pm$ 1.30	7.95 $\pm$ 0.92	43.7 $\pm$ 5.1

This comparison shows a remarkable difference throughout, the most important feature probably being the fact that the coefficient of variability in total branch-length is more than twice as great in *O. rubrinervis* as in *O. lamarckiana*.

*The size and shape of the leaves of Onagra rubrinervis.*—Much more important taxonomically than stature and branching are the leaf-characters, and it is just here that statistical study encounters the most serious obstacles in seeking a satisfactory basis. In the first

place, some of the leaf-characters are incapable of quantitative expression, such as the degree of crinkling of the leaf, which is a striking, though not an absolutely distinctive feature of the leaf of *O. lamarckiana*. Some leaves of *O. rubrinervis* are also crinkled, but it is a gen-

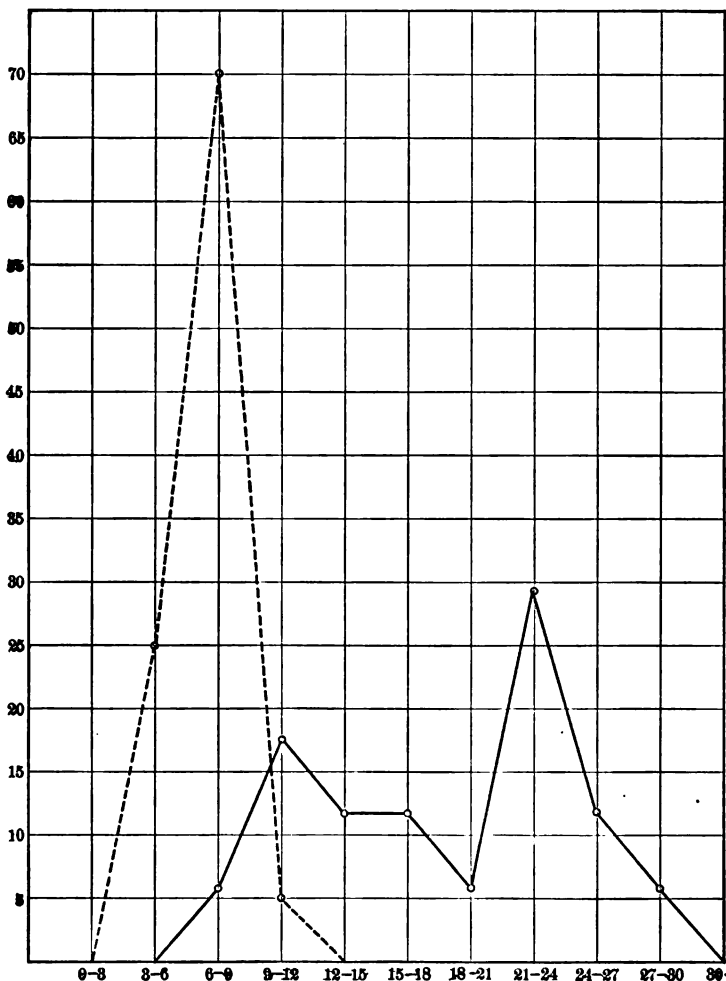


FIG. 5. Variation in total branch-length of *Onagra lamarckiana* and *O. rubrinervis*. *O. lamarckiana*: Range, 8.65 to 8.48 meters; M., 6.68  $\pm$  0.20 meters;  $\sigma$ , 1.85  $\pm$  0.14 meters; C. V., 20.2  $\pm$  2.2 per cent. *O. rubrinervis*: Range, 7.79 to 29.98 meters; M., 18.19  $\pm$  1.80 meters;  $\sigma$ , 7.96  $\pm$  0.92 meters; C. V., 48.7  $\pm$  5.1 per cent.

eral character of the leaf of *O. lamarckiana* and only occasional in *O. rubrinervis*. Other characters, although measurable, present technical difficulties incommensurate with the value of the results, as, for instance, leaf-thickness and degree of pubescence. The leaf of *O.*

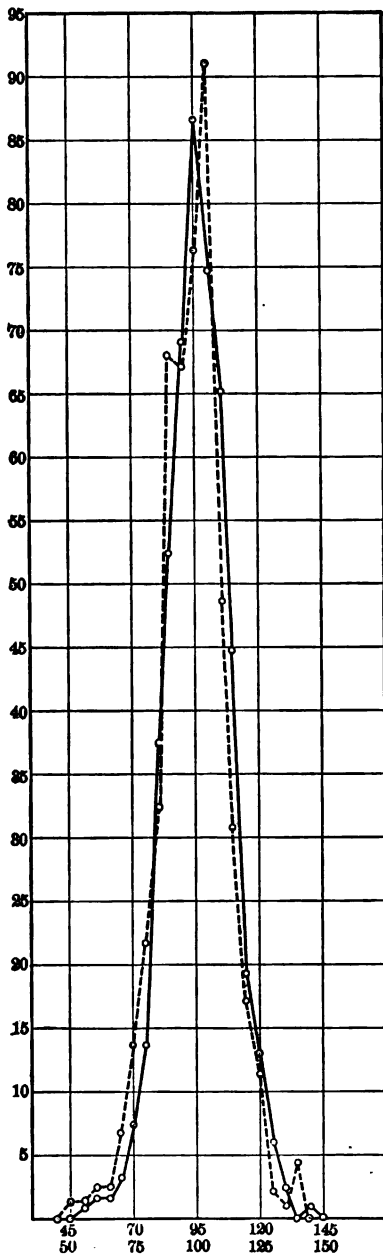


FIG. 6. Variation in leaf-length of *Onagra lamarckiana* and *O. rubrinervis*. *O. lamarckiana*: R., 49 to 137 mm.; M.,  $96.85 \pm 0.42$  mm.;  $\sigma$ ,  $18.08 \pm 0.80$  mm.; C. V.,  $18.60 \pm 0.31$  per cent. *O. rubrinervis*: R., 53 to 142 mm.; M.,  $97.99 \pm 0.84$  mm.;  $\sigma$ ,  $12.87 \pm 0.24$  mm.; C. V.,  $12.62 \pm 0.24$  per cent.

*lamarckiana* is noticeably thicker than that of *O. rubrinervis*. So-called qualitative differences are usually compounds of several measurable characters, any one of which is a wholly unsatisfactory measure of the quality, while only one, two, or several at most of these measurable characters can be dealt with mathematically at a time. Leaf-form is a character of this kind. Not only is the relation of length to breadth important, but the relative position of the widest part of the leaf, the angles of apex and base, and indeed the curvature of the margin at every point from petiole to apex, enter as essential features of leaf-form, and no tangible mathematical expression can be devised to represent it. Confining ourselves to a single measurable character, such as leaf length or breadth, there is still another difficulty which must be met. The leaf is a differentiated organ and there is no exact homology between any two leaves. In a plant which has but few leaves this is strikingly evident, and no leaf on a stem which has ten leaves corresponds exactly to any leaf on another plant of the same species which carries but nine leaves. In plants with numerous leaves, as in the various species of *Onagra*, the degree of differentiation between adjacent leaves is so slight that they may be treated as homotypic without appreciable error, provided as nearly as possible the corresponding parts of the various specimens are used as the source of leaves for the study.

The leaves chosen for this comparative study were taken from a point about two-fifths of the distance from the proximal toward the distal end of the long lateral branches mentioned above as forming a whorl about the base of the main axis. The number of such branches borne by each specimen allowed the collection of a sufficiently large number of leaves by taking them from a very short section of each branch, so that the error due to differentiation is insignificant compared with the "chance" variation. From 20 to 30 leaves were taken from each of 20 specimens of each species, and the width, and the length from the base of the petiole to the apex, were measured in the fresh condition. The length and width were then combined for each leaf in the ratio, width  $\div$  length, this being the simplest possible approximation to a satisfactory mathematical expression for leaf-form. The curves shown in figs. 6, 7 and 8 compare graphically the results of these measurements. It will be noted on reference to fig. 6 that the length of the leaves in the two species is almost identical, while

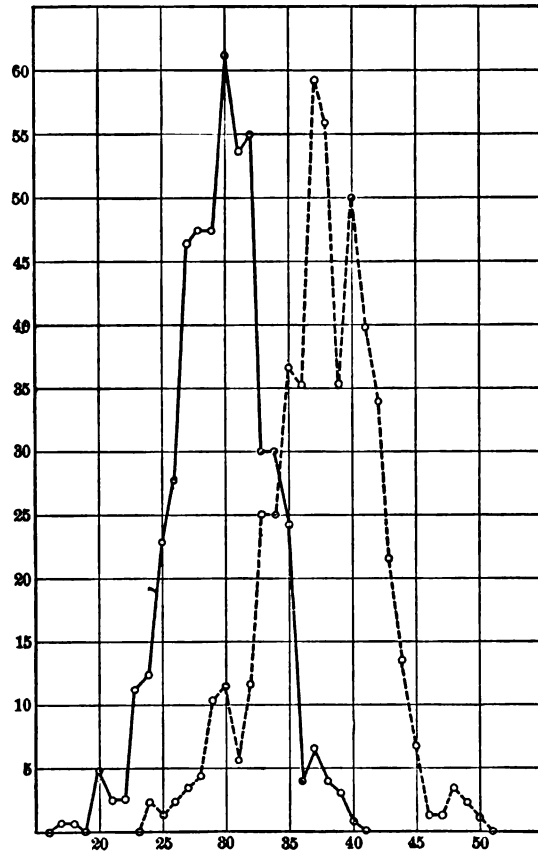


FIG. 7. Variation in leaf-width of *Onagra rubrinervis* and *O. lamareckiana*. *O. rubrinervis*: R., 17 to 40 mm.; M.,  $29.786 \pm 0.006$  mm.;  $\sigma$ ,  $8.589 \pm 0.069$  mm.; C. V.,  $12.07 \pm 0.23$  per cent. *O. lamareckiana*: R., 24 to 60 mm.; M.,  $37.617 \pm 0.137$  mm.;  $\sigma$ ,  $4.248 \pm 0.007$  mm.; C. V.,  $11.29 \pm 0.26$  per cent.

fig. 7 shows that with respect to the width of leaf they are quite different, though not discontinuous. In consequence of the approximate identity in leaf-length the ratio representing leaf-form corresponds closely with the leaf-width in the character and degree of overlapping of its curves, as will be seen on comparing figs. 7 and 8.

The constants of these curves, which represent the variations of the two populations, each taken as a whole, are as follows:

	Mean.	Standard deviation.	Coefficient of variability.
Variation in length of leaf:	<i>Millimeters.</i>	<i>Millimeters.</i>	<i>Per cent.</i>
Onagra lamarkiana .....	96.15 $\pm$ 0.42	13.08 $\pm$ 0.30	13.60 $\pm$ 0.31
Onagra rubrinervis .....	97.99 $\pm$ 0.34	12.37 $\pm$ 0.24	12.62 $\pm$ 0.24
Variation in width of leaf:			
Onagra lamarkiana .....	37.617 $\pm$ 0.137	4.248 $\pm$ 0.097	11.29 $\pm$ 0.26
Onagra rubrinervis .....	29.736 $\pm$ 0.098	3.589 $\pm$ 0.069	12.07 $\pm$ 0.23
Variation in the ratio between width and length:	<i>Per cent.</i>	<i>Per cent.</i>	
Onagra lamarkiana .....	39.964 $\pm$ 0.123	3.811 $\pm$ 0.087	9.53 $\pm$ 0.22
Onagra rubrinervis .....	30.077 $\pm$ 0.084	3.098 $\pm$ 0.056	10.30 $\pm$ 0.20

Considering the great variability of leaves, it would not be expected that two species so closely related would exhibit complete discontinuity in size of leaf or in the ratio between width and length. It is not so much the extreme types of leaves which give to a plant its characteristic appearance and appeal to the systematist, as the type to which the majority of the leaves belong. The mean values of the various leaf-characters for each individual would much more nearly represent the conditions as seen by the descriptive botanist. For this reason it seemed important to compare the means of length, width, and form of leaves in the individual plants of the two species. The results are represented in figs. 9, 10, and 11, and show that there is approximate identity in the mean length of the leaf, but complete discontinuity in both mean widths and the mean ratios of width to length. The constants were not determined for these curves, as an inspection of the curves together with a statement of the ranges will sufficiently indicate the nature and degree of discontinuity present.

The ranges of mean values of the leaf-characters in the individual plants were as follows:

	Length.	Width.	Width+length.
	<i>Millimeters.</i>	<i>Millimeters.</i>	<i>Per cent.</i>
Onagra lamarkiana .....	88.42-112.32	33.74-41.64	34.62-44.41
Onagra rubrinervis .....	86.28-107.15	25.93-32.53	25.30-32.54

It will be noted that the break between the mean values of leaf-width and that between the mean ratios of width to length are slight but sufficient. If a larger number of specimens had been used the range would have been extended somewhat and it is not improbable that they would overlap some, and yet the unsatisfactory character of

the ratio of width to length as a measure of leaf-form would not allow us to infer from such overlapping that the two species are not absolutely distinct with respect to the form of the leaves. This fact will become convincingly apparent upon reference to Plate XXII, in which

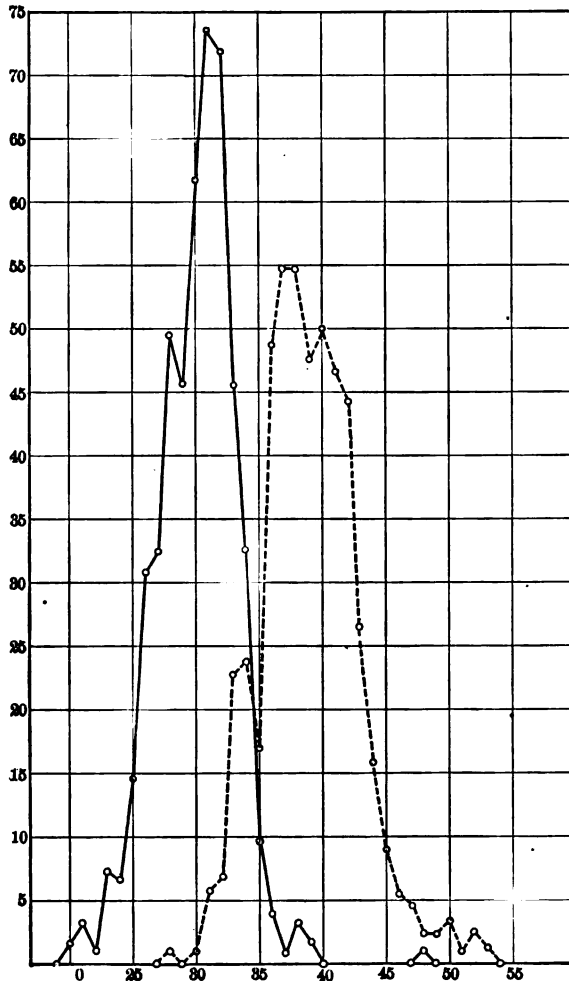


FIG. 8. Variation in ratio of width to length in the leaves of *Onagra rubrinervis* and *O. lamarckiana*, expressed in per cents. *O. rubrinervis*: Range, 20-48; M.,  $30.077 \pm 0.084$ ;  $\sigma$ ,  $8.088 \pm 0.056$ ; C. V.,  $10.90 \pm 0.20$  per cent. *O. lamarckiana*: Range, 28-53; M.,  $39.961 \pm 0.123$ ;  $\sigma$ ,  $8.811 \pm 0.087$ ; C. V.,  $9.58 \pm 0.22$  per cent.

are contrasted the leaves from the specimen of *O. lamarckiana* having the minimum mean ratio and those of the specimen of *O. rubrinervis* having the maximum mean ratio. According to this statistical meas-

ure, these two lots of leaves are the most nearly identical in form of any two plants, belonging to these two species, which were investigated. If to the difference of outlines as shown in the plate could be added the marked crinkling of the *lamarckiana* leaves, a character which disappears on pressing, the discontinuity would be even more obvious.

*Interpretation of statistical results.*—In reviewing the results of this study one feature stands out prominently, which appears to the writer to be of more fundamental significance than the mere determination of the differences in superficial characters of the several species under consideration. This feature will be apparent upon a comparison of the coefficients of variability throughout.

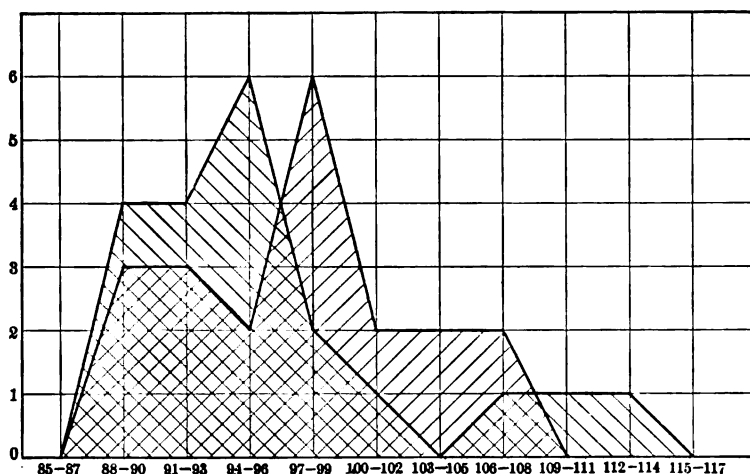


FIG. 9. Variation in the mean length of leaves in *Onagra rubrinervis* and *O. lamarckiana*. Curve for *O. rubrinervis* shaded with lines rising to the right. Range, *O. rubrinervis*, 86.28 to 107.15 mm.; *O. lamarckiana*, 88.42 to 112.82 mm.

The variability of the mutant is significantly higher than that of *Onagra lamarckiana* in four of the six characters considered. In the number of lateral branches, one of the remaining two characters, the excess in favor of *O. lamarckiana* is far within the probable error, and therefore has no significance. Only in regard to the leaf-length of *O. rubrinervis* is there a significantly higher variability in *O. lamarckiana* than in its mutant, and this is a character in which the mutant presents no material difference from its parent, the difference between the mean lengths of leaves in the two species being only 1.1 mm. in excess of the sum of the probable errors.

Probably related to the same causes which determine this greater variability of the mutants is the fact that there is a lower degree of correlation between the length and breadth of the leaves of *O. rubrinervis* than in *O. lamarckiana*. Correlation tables of these two charac-

ters are shown in figs. 12 and 13. The lesser correlation of the former is apparent to the eye in the more scattered distribution of the variates. The coefficients of correlation are as follows: *Onagra lamarckiana*,  $0.7916 \pm 0.0090$ ; *Onagra rubrinervis*,  $0.6604 \pm 0.0119$ . This is simply another way of expressing the fact that the leaf-form of *O. rubrinervis* is more variable than that of its parent-species.

If increased variability and decreased correlation be, as here indicated, a general feature of those characters in which a mutant departs markedly from the parental condition, how is it to be interpreted? It is hinted by Weldon ('02) that these mutants are possibly the result of selection and isolation. No one can deny that there has been selection and isolation in their culture, but it may be questioned whether

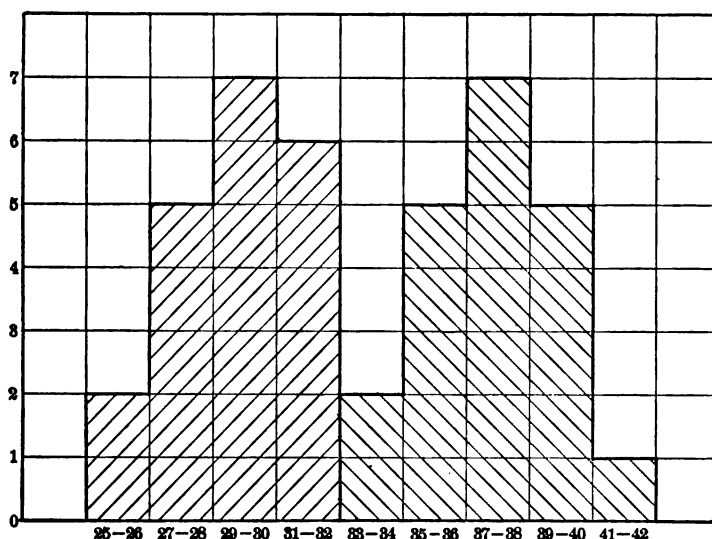


FIG. 10. Variation in the mean width of leaves of *Onagra rubrinervis* and *O. lamarckiana*. Curve for *O. rubrinervis* shaded with lines rising to the right. Range: *O. rubrinervis*, 25.98 to 32.58 mm.; *O. lamarckiana*, 33.74 to 41.64 mm.

these processes have been carried on to such an extent as to explain the peculiar behavior of the mutants as compared with that of an extreme variate. This question will not be satisfactorily answered until a newly arisen mutant shall be subjected to various conditions of cross and self fertilization, and the results are studied statistically. It seems fair to assume that there has been a more discriminating selection in the case of the several mutants than in *O. lamarckiana*. It is therefore something of a surprise, if Weldon's suggestion be true, to find the latter less variable in nearly every character studied. This surprise is due to what may be a false assumption, namely, that selection necessarily operates to lessen variability. Is it not conceivable



that the selection of an extreme condition may result in increased variability even after several generations?

The supposed effects of self and cross fertilization can hardly be assumed as of any consequence in this connection, for both species have been self-fertilized during a number of generations. Just what effect this has had upon their variability is not known. De Vries does not think that cross-fertilization, even hybridization, has any appreciable influence on the frequency of origin of a given mutation in a mutating species. (De Vries, 1901, p. 211-212; 1903, p. 425-426.)

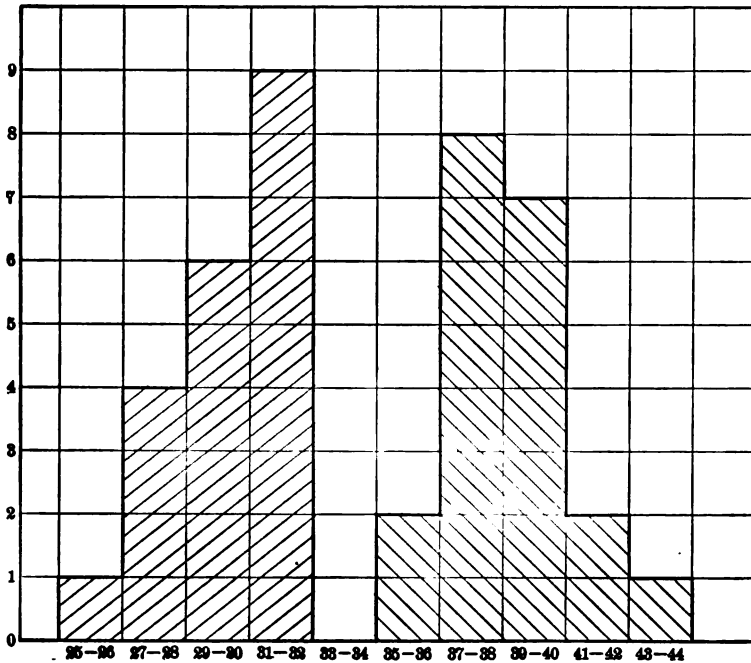


FIG. 11.—Variation in the mean ratio between width and length of leaves in *Onagra rubrinervis* and *O. lamarckiana*. Curve for *O. rubrinervis* shaded with lines rising to the right. Range: *O. rubrinervis*, 25.80 to 32.54 per cent.; *O. lamarckiana*, 34.63 to 44.41 per cent.

Weismann (1892) maintained in his earlier works that all hereditary variation is due to cross-fertilization, but more lately he has withdrawn from this extreme position, and now considers amphimixis “nicht als die eigentliche Wurzel der Variation selbst, denn diese kann unmöglich auf einen blossen Austausch der Ide, sie muss vielmehr auf einer Veränderung der Ide beruhen.” He even looks upon cross-fertilization as a process by which the range of variation is lessened, and the variable forms which he thinks may arise at each “Neuanpassung,” are condensed into a species and rendered constant. (Weismann, 1902, 2:235.)

Darwin performed a large number of experiments to test the effect of self and cross fertilization, but his object was to determine the advantages or disadvantages as measured by height, productivity, etc., rather than the effect on variability. The number of specimens used by him in each species studied was hardly sufficient to allow conclusions of value regarding variability, but he infers that variations are primarily

		X <sub>2</sub>	-9	-8	-7	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5	6	7	8	9		
			50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140		
			55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140	145		
X <sub>1</sub>																							
-12	17				1																		1
-11	18			1																			1
-10	19																						0
-9	20			1		1	3	1															6
-8	21		1					1			1												3
-7	22				1	2																	3
-6	23						2	2	7	2		1											14
-5	24						1	2	6	2	1	2			1								15
-4	25						3	2	6	6	3	5	2			1							28
-3	26							3	5	6	11	3		1	2	1	1	1					34
-2	27							2	15	11	7	9	6	3	3				1				57
-1	28							3	4	10	8	16	5	9	1	2							58
0	29							1	2	11	19	10	3	6	5	1							58
1	30							1	13	12	10	16	10	8	1	2		1		1			75
2	31				1				2	11	18	21	6	3	1	1	1	1					66
3	32								1	8	17	20	8	7	3	3	1						68
4	33									1	9	9	7	6	3	2							37
5	34										1	6	15	5	7	1	2						37
6	35									2	3	4	13	5	2	1							30
7	36										1		1	3									5
8	37									1	1		1	2	1	2							8
9	38													2		1	2						5
10	39														2	1	1						4
11	40																1						1
			1	2	2	4	9	17	46	64	85	106	92	80	55	24	16	7	3	0	1		614

FIG. 12. Correlation table of length and width of leaf in *Onagra rubrinervis*.  
Width of leaf subject, length relative;  $\rho = 0.6604 \pm 0.0119$ .

due to differences of environmental conditions, and that cross-fertilization tends to produce uniformity when these variations are slight, and to increase the diversity when the variations are considerable. These questions need thorough reinvestigation, and their discussion is futile until such investigation is made. (Darwin, 1876, p. 452.)

If the *Onagra* mutants are not the result of selection and isolation, acting within the field of applicability of known laws of variation and heredity, but are really, as they have been called by certain German writers, "correlation-breakers," may not the increased

variability and decreased correlation be explained by the newness of the species, which may be assumed to want that perfect adjustment to their surroundings which an older species has acquired through the cumulative effects of long-continued adaptive reactions, aided by natural selection—*i. e.*, by the elimination of the unadapted? This

		X <sub>2</sub>	-9	-8	-7	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5	6	7	8	9	
			45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	
			50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140	
X <sub>1</sub>																						
-13	24		1					1														2
-12	25			1																		1
-11	26			1	1																	2
-10	27					1	1		1													3
-9	28					1	1		1	1												4
-8	29						1	2	3	2	1											9
-7	30						1	2	2	2	3											10
-6	31							1			2	2										5
-5	32								2	2	4		2									10
-4	33						1	1	6	3	4	4	3									22
-3	34							1	1	5	8	3	3	1								22
-2	35							1	2	4	9	6	1	4	3	1		1				32
-1	36						1	1	1	2	5	10	4	5	1		1					31
0	37							1		3	11	9	11	8	5	3	1					52
1	38							1		4	3	11	10	16	3	1						49
2	39									3	7	7	8	4	1	1						31
3	40									6	4	9	6	12	3	4						44
4	41										1	8	10	5	5	1	4	1				35
5	42										2	7	9	5	3	2	1			1		30
6	43								1			1	8	4	2	2				1		19
7	44												3		6		2		1			12
8	45												1	1	1	1	2					6
9	46														1							1
10	47																			1		1
11	48																2			1		3
12	49													1					1			2
13	50													1								1
			1	1	2	2	6	12	19	28	60	50	67	80	43	27	15	10	2	1	4	439

FIG. 13. Correlation table of length and width of leaf in *Onagra lamarckiana*. Width of leaf subject, length relative;  $\rho = 0.7916 \pm 0.0080$ .

question also can be answered only by experimentation and observation continued through a series of years.

It appears highly desirable that the statistical study of *O. lamarckiana* and its mutants should be continued during a series of years, and that similar studies should be made of other mutating and mutant species. The exact status of the mutants with regard to their variability and capacity for self-maintenance may be most conclusively determined by the use of the methods entailed in such work.

## GENERAL SUMMARY.

A brief *résumé* of the more salient features of the foregoing paper will serve to emphasize the contributions made to the subject during the course of the experimental work described.

A continuance of the effort to trace the nativity of *O. lamarckiana* has resulted in the discovery of records and specimens that appear fairly conclusive that it is a true and independent species native to America, although the matter is not decided with the finality afforded by living specimens observed in the field. That this species has remained unchanged during a period of a hundred and sixteen years is established beyond doubt, and renders the matter of its nativity of comparatively little importance as to the standing of the mutants derived from it. Perhaps no plant is known in which the purity of the strain has been so critically examined as Lamarck's evening-primrose. Some of the mutants are derivatives, most of which have become separated from the parent-form by the acquisition of new characters, while others are of a retrogressive character. Many of the new unit-characters displayed are not known in any of the other members of the natural group, and thus may not be regarded as degressive acquisitions, or as due to the retraction of a retrogressive step taken in the previous history of the parent-species.

The material used as *O. biennis* in the investigation described in *Die Mutationstheorie* proves to be a large-flowered species, which has probably been known to many workers as *O. biennis grandiflora*. The uniformly unilateral character of the cross between this species and *O. lamarckiana* (*O. lamarckiana*  $\times$  *O. biennis grandiflora*) which was an untypic hybrid very similar to the pollen-parent, a result which led De Vries to the conclusion that *O. lamarckiana* was a direct derivative of the latter, probably by mutation. A re-examination of the evidence, however, recalls that the cross with *muricata* was similarly unilateral to the latter when used as a pollen-parent, and it is evident that too much weight must not be given to the conclusion in question until confirmatory evidence is obtained.

A consideration of the groupings of characters leads to the conclusion that *O. grandiflora* Ait., *O. lamarckiana* Ser., and *O. argillicola* MacKenzie are much more closely related to one another by anatomical characters and physiological traits than to *biennis* or any other member of the genus. Furthermore, the ranges of the three species mentioned appear to be more or less identical, or overlapping.

*O. grandiflora* Ait. had been seen by but few botanists in a living condition in America, and its place in the American flora had become

a matter of much doubt, but field expeditions guided by descriptions from Bartram's travels in 1776 resulted in a rediscovery of the species in a spot not far from the original locality. This found, the confusion which had arisen as to the separation of this species and *O. lamarckiana* is cleared up.

The cultures of the evening-primroses made in the New York Botanical Garden show that two or more elementary species are grouped under some of the specific names as ordinarily accepted. The failure to recognize these elements has resulted in the prevalent opinions as to the wide range of fluctuating variability exhibited by these plants. This is especially true of *O. biennis*, which has enjoyed a reputation for variation not justifiable by systematic and orderly observations made on plants grown under various conditions. One of the forms, apparently typical of the true *O. biennis* now under cultivation, is in a mutative condition, but description of the derivatives is reserved until they have completed a cycle of development.

*O. cruciata* as it exists at the present time in the cultures in the New York Botanical Garden, and in the Botanical Garden of Amsterdam is composed of three elementary species, which are fairly distinct and without intergrading forms. A careful analysis of the occurrence of the group leads to the inevitable conclusion that one of the forms is in a mutating condition.

It is evident that in the investigations of native species for possible mutating forms, the first and most important task to be completed is that of the resolution of the forms selected into their elementary constituents. Otherwise the seed obtained from plants belonging to separate strains might well give an appearance of variability not justifiable by the facts. Mutations, therefore, may be taken as properly authenticated only when appearing in guarded pedigree-cultures from seeds produced by a known individual, which should be preserved for comparison. Discussions of mutants secured under other conditions may serve an important purpose in offering clues which will be useful in the selection of research material, but can have no direct or actual value as a contribution to the subject.

The evening-primroses of eastern North America, from which probably all of the forms cultivated in Europe are derived, may be divided into two groups—a group including *O. biennis*, *muricata*, *oakesiana*, and *cruciata*, in which the flowers are comparatively small, and in which self-pollination is possible and frequent. The second group, including species native to a region farther south, comprises *O. argillicola*, *O. grandiflora*, and *O. lamarckiana*, in which the flowers are large and the stamens are much shorter than the pistil, a condition which with some accessory structures favors cross-pollination.

The hybrid *O. lamarckiana*  $\times$  *O. cruciata* consisted of a single type in which the characters of the pollen-parent were largely dominant, although none of them were transmitted unchanged. A singular union of characters was shown in the relative lengths of the stamens and pistils, a feature favoring cross and self fertilization. Some of the flowers bore stamens shorter than the pistils, while in others these organs were of equal length. Many of the modifications of the predominating characters were dependent upon and were modified by the alterations in the general stature of the plant. This hybrid corresponds quite closely with the descriptions of *O. cruciata varia*, a supposed hybrid of *O. cruciata* and *O. muricata* given by De Vries.

The hybrid of *O. lamarckiana*  $\times$  *O. biennis* was of a pleiotypic character, being composed of four well-differentiated types with no intergrading forms. This result differs widely from that obtained by De Vries in hybrids with *O. biennis grandiflora* and *O. muricata* as the pollen-parent. In both of the last-named instances the result of the cross was a unotypic hybrid closely unilateral to the pollen-parent. In *O. lamarckiana*  $\times$  *O. biennis* some characters of both parents were transmitted to all of the four types of the hybrid, but the greater number of the active characters were those of the pollen-parent.

A remarkable predisposition or weakness to the attack of a fungal parasite was exhibited by one of the types. The habit of inequality of growth of the laminae resulting in crinkling, characteristic of *lamarckiana*, was transmitted to all individuals of the four types of the hybrid. The symmetrical form of the terminal rosettes of *lamarckiana* was transmitted unchanged to two of the types. No other characters of the pistil-parent were inherited in their entirety, although a number of qualities, approximating those of *lamarckiana* sufficiently to be termed "dominant" by some authors, were seen. Three of the types were goneoclinic to the pollen-parent, while the fourth (No. 2.24) may be fairly taken as furnishing an example of an intermediate form, so far as such estimations may be taken to be of value. The zigzag stem, No. 2.27, is an example of the dominance of a feature usually latent in the pistil-parent, but exhibited by one of its mutants, *rubrinervis*. The capacity for self-fertilization was dominant in three of the types, but in the fourth a variability between cross and self fertilization was indicated by the varying relative lengths of the stamens and pistils. It is to be noted in this connection that *O. brevistylis*, one of the mutants of *O. lamarckiana*, has a pistil shorter than its stamens, and is therefore adapted to self-fertilization, although no actual physiological predisposition in the matter is found.

The recurrence of known mutants of *O. lamarckiana* was observed. *O. rubrinervis* appeared among the hybrid progeny of *O. lamarckiana*  $\times$  *O. biennis*, in which imperfect castration had been accomplished and the parental strain appeared in the cultures. It appears therefore that the mutant may be considered as a derivative of the one parent purely, although the possibility is not excluded that it might have come as a hybrid strain, as has been observed by De Vries in several crosses. Better authenticated mutants were seen to arise from seeds obtained from purely fertilized plants of *O. lamarckiana* grown in the botanical garden at Amsterdam in 1901; also from seeds of the same species gathered in the New York Botanical Garden in 1903 after similar precautions had been observed. *O. albida*, *scintillans*, *gigas*, *oblonga*, *subovata*, and *O. elliptica* were found among the mutants, offering evidence of the indubitable occurrence of the mutants in purely fertilized seeds, and also that *O. lamarckiana* has not reached the end of its mutative period. Furthermore, seven forms not definitely assignable to any of the known mutants of this parent were found, showing that the range of the mutability of the species had been extended by unknown causes, but which were included in an environment of cultural conditions extremely favorable to rapid and vigorous growth and development. It seems safe to assume, therefore, that mutation is induced, or at least increased, by favorable, not adverse conditions, though the duration of the experiments has not been sufficient to permit an analysis of this phase of the subject.

*O. gigas*, the species most recently tested in the mutation-cultures in New York, was seen to agree in stature and habit with the individuals grown in the original locality at Amsterdam. Only about half of the individuals could be brought into bloom during the first season, although it was extended to ten months by special methods of culture—a fact in accord with the behavior of the plant in De Vries's cultures. The constancy of the species also extends to its variability as to the forms of the leaves, an attribute also previously recognized.

The results of the statistical studies show that some of the unit-characters of the mutants have a much greater variability than the corresponding features of the parent-form, and the greater amplitude of the fluctuations is coupled with a decreased correlation.

Thus the coefficient of variability of the height of the shoot of *nanella* is  $31.84 \pm 3.16$  per cent, while that of *lamarckiana* is  $5.37 \pm 0.44$  per cent. The coefficient of variability for the number of branches of *rubrinervis* is  $15.0 \pm 1.7$  per cent, and for the total length of the branches is  $43.7 \pm 5.1$  per cent, and for the ratio between width and length of the leaves is  $10.30 \pm 0.20$  per cent; for the number of

branches of *lamarckiana*  $15.7 \pm 1.7$  per cent, for the total length of the branches  $20.2 \pm 2.2$  per cent, and for the ratio between the width and length of the leaves  $9.53 \pm 0.22$  per cent.

The great variability of the mutants does not, however, seem to result in any diminution of the gap that separates them from the parent form, and no movement in this direction has been observed in the long period which has elapsed since the new species came into existence. Thus the heights of *O. nanella* group themselves about the mean value of  $22.81 \pm 1.02$  cm., with a range from 7 to 35 cm., while those of *O. lamarckiana* group themselves about the mean of  $88.68 \pm 0.55$  cm., with a range from 77 to 96 cm. The number of branches per individual of *lamarckiana* ranged from 11 to 25, while that of *rubrinervis* was 34 to 62. The actual discontinuity is somewhat more fully expressed, however, by a comparison of the numerous features which elude measurements to be seen in Plate XXII, in which leaves from the specimens of *lamarckiana* and *rubrinervis* which approached each other most nearly are shown. The actual discontinuity between the retrograde variety, *O. nanella*, and its parent in the leading feature of height of stem is even more marked than the gap between the various unit-characters of *rubrinervis* and *lamarckiana*.

Recurring again to the amplitude of the fluctuations in the mutants, it is to be said that it is doubtless much greater in the leaf-forms of the retrograde variety, *O. nanella*, than in any which have been measured, if the entire mass of foliage is taken into account, since in a certain mid-stage in the rosette it is practically impossible to distinguish it from the parent, although fully distinct as to form and size of the leaves in the very young and very old rosettes. The very range of variation may be in itself a character of the mutants, in which case no reason could be given for its existence, any more than reasons could be given for the existence of any other unit-character. Similar difficulties might be encountered in seeking an explanation of the comparative amplitude of variation of any group of related forms.



**BIBLIOGRAPHY.**

AITON, WILLIAM.

1789. Hortus kewensis; or, a catalogue of the plants cultivated in the Royal Botanic Garden at Kew. 2: 2. London, 1789.

BARTON, WILLIAM P. C.

1821. A flora of North America. 1: 21-24, pl. 6. Philadelphia, 1821.

BARTRAM, WILLIAM.

1793. Travels through North and South Carolina, Georgia, East and West Florida, the Cherokee country, the extensive territories of the Muscogulges or Creek Confederacy, and the country of the Chactaws. Dublin, 1793 (reprinted from the Philadelphia edition of 1791).

CHAPMAN, A. W.

1860. Flora of the Southern United States. New York, 1860.  
1884. Flora of the Southern United States. Second edition. New York, 1884.  
1897. Flora of the Southern United States. Third edition. Cambridge, Mass., 1897.

CORRENS, C.

1903. Ueber die dominirenden Merkmale der Bastarde. Ber. d. Deut. Bot. Gesell., 21: 133, 1903. Also, Weitere Beiträge zur Kenntniss der dominirenden Merkmale und der Mosaikbildung der Bastarde. Same journal, 21: 195, 1903.

DARWIN, CHARLES.

1876. The effects of cross- and self-fertilization in the vegetable kingdom. 482 pages. London, 1876.

DE VRIES, HUGO.

1901. Die Mutationstheorie. Versuche und Beobachtungen über die Entstehung von Arten im Pflanzenreich. Erster Band. Die Entstehung der Arten durch Mutation. 648 pages, 8 plates. Leipzig, 1901.  
1902. Die Mutationstheorie. Versuche und Beobachtungen über die Entstehung der Arten im Pflanzenreich. Zweiter Band. Die Bastardierung. Erste Lieferung. Pages 1-240. Leipzig, 1902.  
1903. Die Mutationstheorie. Versuche und Beobachtungen über die Entstehung von Arten im Pflanzenreich. Zweiter Band. Elementare Bastardlehre. Pages 241-751, 4 plates. Leipzig, 1903.  
1905. Species and varieties: their origin by mutation. Edited by D. T. MacDougal, xviii 847 pp. Chicago and London, 1905.

DOMBRAIN, H. H.

1862. Lamarck's evening primrose, *Oenothera lamarckiana*. The Floral Magazine, 2: plate 78 (with accompanying text). 1862.

GALTON, FRANCIS.

1889. Natural inheritance. ix + 259 pp. London, 1889.

HURST, C. C.

1900. Notes on some experiments in hybridization and cross-breeding. The Journal of the Royal Horticultural Society (London), 24: 90-126. Ap., 1900.

LEMAIRE, CHARLES.

1862. *Oenothera Lamarckiana*. L'Illustration Horticole, 9: plate 318 (with accompanying text). 1862.

MACDOUGAL, D. T.

1903. Mutation in plants. *The American Naturalist*, 37: 737-770. N 1903.  
[1 Ja., 1904].

PETER, A.

1884. Tabelle über die Procentsätze der bei den Bastarden der *Piloselloiden* unterschiedenen Merkmale. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, 5: 246-251. 1884.

PURSH, FREDERICK.

1814. *Flora Americae Septentrionalis; or, a systematic arrangement and description of the plants of North America.* 261. London, 1814.

VAIL, ANNA MURRAY.

1905. *Onagra grandiflora* (Ait.), a species to be included in the North American Flora. *Torrey*, 5: 9-10, Ja. 1905.

WELDON, W. F. R.

1902. Professor de Vries on the origin of species. *Biometrika*, 1: 365-374, .  
Ap., 1902.

WEISMANN, AUGUST.

1892. Aufsätze über Vererbung und verwandte biologische Fragen. 848  
pages. Jena, 1892.  
1902. Vorträge über Descendenztheorie gehalten an der Universität zu  
Freiburg im Breisgau. Zweiter Band. 462 pages, 3 plates. Jena,  
1902.







**STAGES IN THE DEVELOPMENT**

**OF**

**SIUM CICUTAEFOLIUM**

**BY**

**GEORGE HARRISON SHULL**

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PLATE I.



*Sium cicutaefolium* Gmel. A jar of seedlings, photographed at the University of Chicago, October 10, 1903, by Dr. W. J. G. Land; spring-growth of an old plant, photographed at Lockport, Ill., May 16, 1903, by W. E. Praeger; and a flowering-stem photographed at South Chicago, September 22, 1903.

# STAGES IN THE DEVELOPMENT OF SIUM CICUTAEFOLIUM.

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BY GEORGE HARRISON SHULL.

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The juvenile forms of leaves have been believed to be so related to the evolutionary history of a plant as to indicate the form of leaf possessed by its ancestors and to furnish satisfactory evidence of the closeness of relationship between allied species. It is impossible, in most cases, to determine the ancestors of any species, and it is likewise impossible, therefore, to demonstrate a close parallel between ontogeny and phylogeny. As there is in both processes the development from some simple condition to one and the same complex condition, namely, the climax type of leaf of the present adult plant, we can scarcely escape the belief that such a parallel does exist in many cases; but how safely or in how minute detail we may reason from ontogeny to phylogeny may well be considered an open question.

The hypothesis of von Baer (1828) has proved a very suggestive one, and, like most suggestive hypotheses, has been given a much wider application than its author would have been willing to sanction. Von Baer did not assume that the adult characters of the ancestors occur as larval or juvenile characters in the descendants, but that the same larval stages occur in both, a given stage appearing earlier in the descendant than in the ancestor. The idea that larval and juvenile characters agree with ancestral *adult* characters was an old conception which was rehabilitated by Louis Agassiz (1848-1849) and became crystallized in the epigram of Haeckel (1866), which is now universally known as the "Law of biogenesis"—that "ontogeny repeats phylogeny."\*

Great stress was laid upon this hypothesis by Hyatt, Cope, and others who have used it as a most important principle in disentangling difficult phylogenetic problems. More recently Jackson (1899) has called attention to the fact that in organisms having periodically interrupted

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\*For a history of the development of the idea of repetition see Hyatt, A., "Cycle in the life of the individual and in the evolution of its own group." The law of repetition is there called "Agassiz's law of palingenesis." See also Glaser, O. C., "The law of von Baer."

growth, modified characters which he believes to be atavistic occur in definite parts of the organism, particularly in the region where resumption of growth takes place. These local modifications he calls "localized stages" and says that the equivalents of these stages "are to be sought in the adults of ancestral groups." In three recent papers in the *American Naturalist*, Cushman (1902, 1903, 1904) gives the result of studies similar to those of Jackson, and, besides presenting evidence that at the resumption of growth in perennial herbs in the spring these atavistic modifications occur, lays stress upon senescent stages as showing even more primitive conditions than are to be found in the seedling. It may be said, in passing, that this view of the significance of senescent stages does not fully accord with that of Hyatt (1890, pp. 78, 79; 1897, p. 221), who looked upon senescent stages as indicative of the course any species in question will pursue in the process of degenerative evolution. In Hyatt's view the senescent stages have a prophetic instead of an historic significance, though he recognized, of course, that there are many resemblances between the senescent and the juvenile series.

If the propositions of Hyatt and Cope, of Jackson, and of Cushman are all true, there should be at least three regions in any perennial plant which will agree in presenting ancestral characters—the juvenile leaves following the cotyledons, the earliest formed parts at each renewal of vegetative activity, and the senescent stages approaching and accompanying the inflorescence. In numerous cases there is a general agreement in the forms passed through at these three regions, and no inconsistency arises when they are all looked upon as atavistic, though the mere fact of agreement in the several regions can not be taken as in itself convincing evidence that these characters agree with the adult characters of some ancestral group. On the other hand, certain plants do not show the same modification of leaf-form in the inflorescence that is found in the "nepionic" leaves of the seedling, and it becomes at once evident that no reliance can be placed upon the forms of leaf occurring in any of these regions as having more than the most general significance as indications of ancestral characters.

A plant which most strikingly illustrates this fact is the hemlock water-parsnip (*Sium cicutaefolium* Gmel.), which presents a great range of leaf-form and passes rather rapidly, sometimes suddenly, from one form to another without repetition, so that each of the regions supposed to tell of ancestral conditions tells a different story. This fact is illustrated in a general way by Plate I.

The seedling of *Sium cicutaefolium* is so different from the adult plant that, except when the two are associated together, its identity

would scarcely be suspected. I am not aware that this seedling has ever been described, and the striking variations in the form of the juvenile leaves make description difficult.

The cotyledons are quite similar to those of many other of the Umbelliferae, being narrowly oblong or elliptic oblong, rather acutely rounded at the apex, and tapering gradually into a petiole at the base. The petiole and blade together are 1.5 to 2 cm. long and the blade is 2.5 to 4 mm. wide.

The early "nepionic" leaves are extremely variable, but it is rare that they do not consist of a single blade constructed on a somewhat palmate plan. The blade is usually of rounded form and quite variously notched, cut, or lobed. In order to facilitate a systematic investigation of the variation in these leaves they were divided into several more or less artificial groups. The first nepionic leaf in more than 120 unselected individuals\* presented forms which were placed in six of these categories, as follows:

(a) About 10.5 per cent were divided palmately into five nearly equal lobes, one or two of which were sometimes slightly notched.

(b) Twenty per cent were 3-lobed, with the middle lobe 2-notched and the lateral lobes each bifid.

(c) The leaves in the third group were likewise 3-lobed, but the lobes were quite variously notched. Over 28 per cent of the seedlings had the first leaf of this description.

It will be noted that the form of leaf described under (b) is simply a special case of (c), and was separated from it because this was the only form of trilobed leaf which could be so definitely characterized, and because this simple definite type of trilobation is almost wholly limited to the first nepionic leaf.

(d) Over 15 per cent showed the tendency to trilobation by a single cleft on one side, unmatched by a cleft on the opposite side. These will be spoken of as "half 3-lobed leaves." They pass gradually into a form having one lateral leaflet, and these two conditions were kept together in a single category.

(e) Nearly 25 per cent had a generally rounded, ovate or cordate form, merely dentate, or irregularly cleft in a manner which did not suggest trilobation.

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\*The seedlings were taken up on two small clumps of earth from their native habitat near Robey, south of Chicago, Illinois. The individual seedlings were carefully separated and all were transplanted about 3 cm. apart in a regular pattern in glass dishes. The point of departure for each dish was marked and a number assigned to each seedling, so that drawings made from time to time could be labeled in a manner to allow the progress of each individual to be followed.

(f) Less than 2 per cent had one pair of lateral leaflets, and may perhaps be looked upon as an extreme form of the 3-lobed condition of category (c), but (c) is essentially palmate, while (f) is essentially pinnate.

A glance at Plate II will show, better than description, the variability of the first nepionic leaf, and it will also show how truly gratuitous is the division into the categories just described. The leaves were chosen at random from the material at hand, but when more leaves were chosen than could find place in the plate the less dubious forms were discarded in order to show the real difficulties of such a classification and to give a clue to the personal equation of the writer in distinguishing the several categories. The letters A, B, C, etc., illustrate the categories described above under (a), (b), (c), etc.

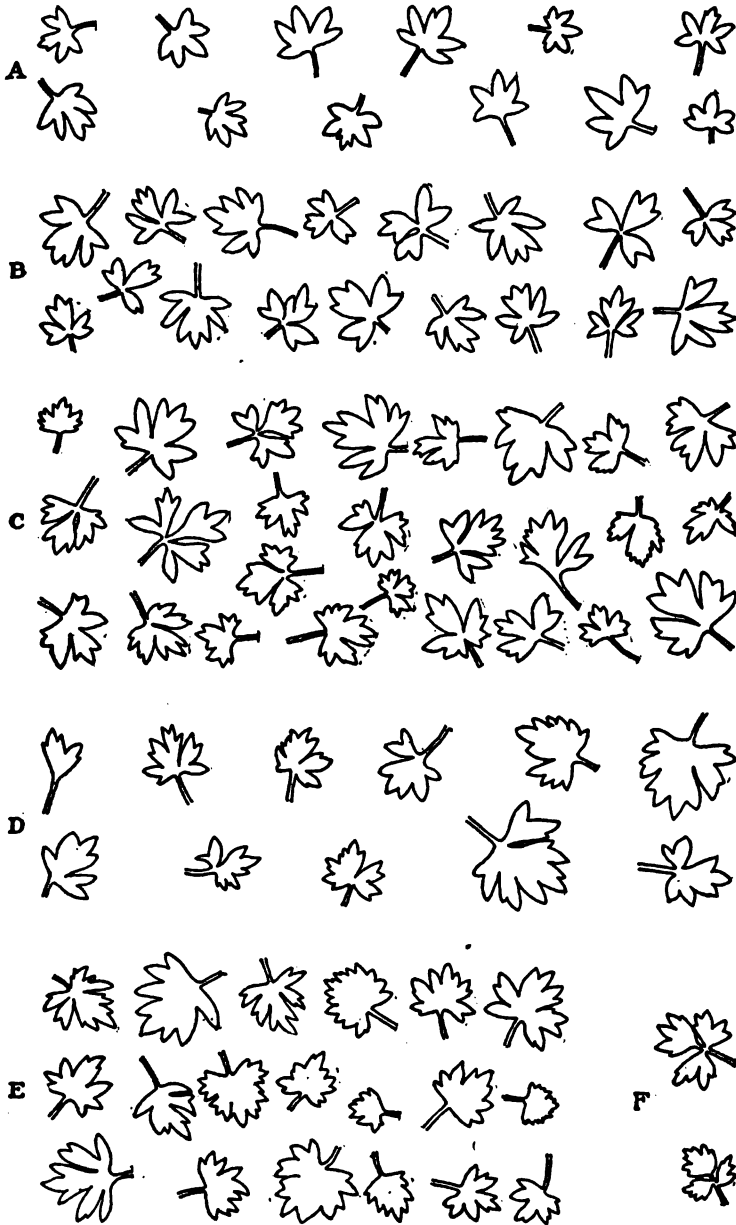
The first two classes, (a) and (b), are characteristic of the first nepionic leaf. With the exception of these two forms, all the categories described above are represented in each succeeding leaf up to the sixth, and perhaps occasionally in the seventh, and in these later leaves the various types are much more definitely distinguishable, so that there is rarely any question as to where any leaf should be classed. With rare exceptions every leaf after the sixth is pinnate and shows a marked contrast to the great variability of the first leaf, so that in the eighth leaf a very large majority have three pairs of lateral leaflets which closely resemble the typical stem-leaves of the species, except in texture and in the more ovate form of the terminal leaflet.

In the second nepionic leaf (Plate III, 2) trilobation was found in only a little over 15 per cent of the seedlings, or about one-third as frequently as in the first nepionic leaf, but the half 3-lobed form had increased from 15 per cent to 18 per cent, the unlobed or irregularly lobed form had increased from 25 per cent to over 61 per cent, and the form with one pair of lateral leaflets from 1.6 per cent to about 5 per cent. Just as the 3-lobed form was the modal condition of the first nepionic leaf, the unlobed form was the modal condition of the second.

The third nepionic leaf (Plate III, 3) showed a partial return to the 3-lobed condition, and nearly 24 per cent of the specimens were so characterized. The half 3-lobed form occurred in over 22 per cent, the unlobed or irregularly lobed form in 39 per cent, and the number having a pair of lateral leaflets had increased from 5 per cent in the second leaf to over 15 per cent in the third. Here, although there was an increase in each of three categories at the expense of the unlobed form, the latter was still the modal form of leaf.

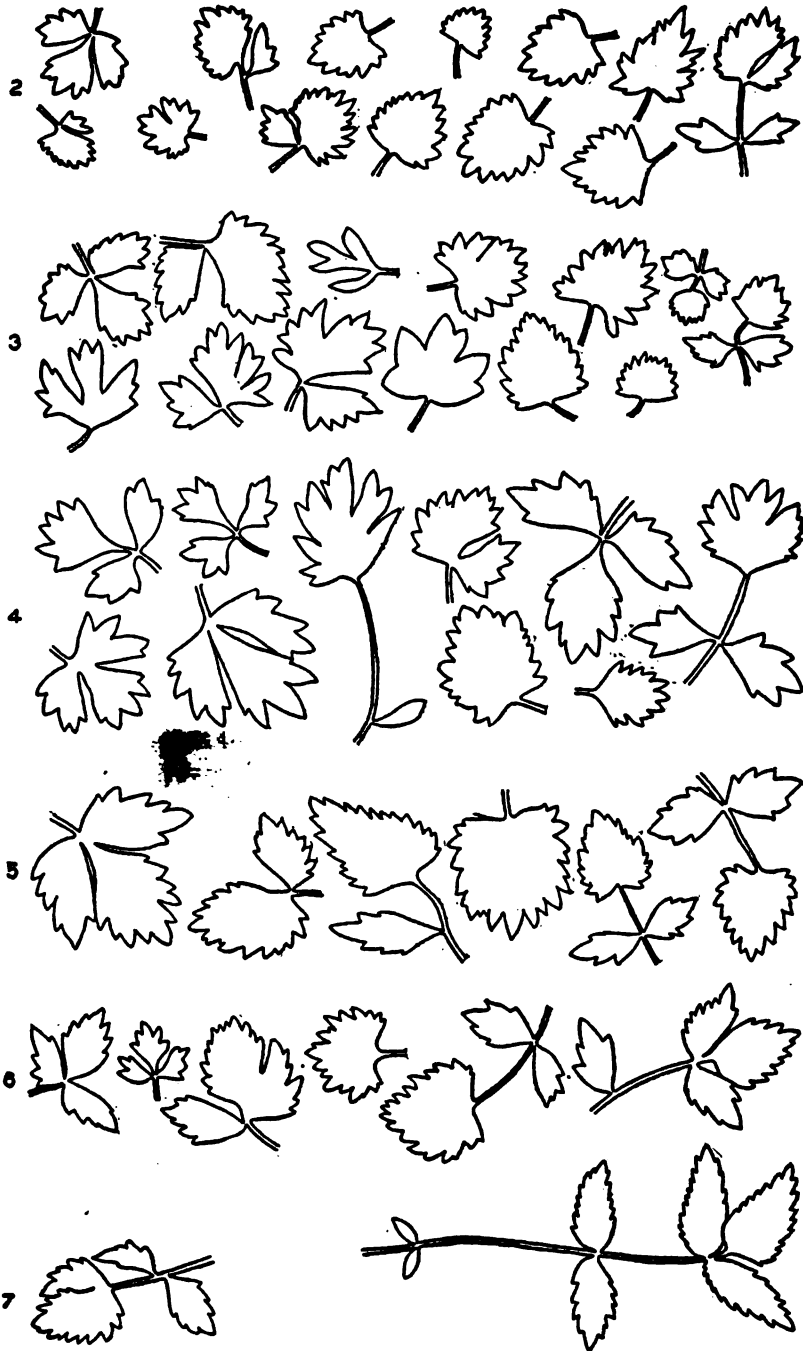
The fourth leaf (Plate III, 4) was 3-lobed in 24 per cent, half 3-lobed in 15 per cent, unlobed or irregular in nearly 23 per cent, and pinnate

PLATE II.



Variation in the first "neplonic" leaf of *Sium cicutaefolium*. Eight-ninths natural size. All drawn from nature with an Abbe camera. A, B, C, etc., correspond to (a), (b), (c), etc., in the text.

PLATE III.



Variation in successive seedling-leaves of *Sium cicutae-folium*, from the second to the seventh. Eight-ninths natural size. Drawn from 'nature with an Abbe camera. Numbers represent the position of each group of leaves in the seedling.

with one pair of lateral leaflets in 30 per cent, this simplest type of pinnation now becoming the modal form of leaf.

In the fifth leaf (Plate III, 5) the percentages of all the types of single blades had considerably decreased and the pinnate had increased, so that now only 4.3 per cent were 3-lobed and the same number half 3-lobed, 17 per cent were unlobed or irregular, and more than 71 per cent had one pair of lateral leaflets, while a little more than 2 per cent had two pairs of leaflets.

The sixth leaf was 3-lobed in only 3.5 per cent of the specimens examined and the same number were unlobed or irregular. About 7 per cent were half 3-lobed, nearly 45 per cent had one pair of leaflets, and over 41 per cent had two pairs of leaflets.

In the seventh leaf none were observed which had not at least one pair of leaflets, though it is not improbable that single blades may occur occasionally in the seventh leaf. The specimens in hand showed 27.5 per cent with one pair of leaflets, over 51 per cent with two pairs of leaflets, and 21.6 per cent with three pairs of leaflets, so that in the seventh nepionic leaf the form with two pairs of lateral leaflets is the modal form.

The eighth leaf presents the same three forms, but only a little over 9 per cent had a single pair of lateral leaflets, 18 per cent had two pairs, and nearly 73 per cent had three pairs.

For more ready comparison these percentages are brought together in the following table. The modal form (empirical) in each leaf is given in full-faced type. The variation of leaf-form occurring in each succeeding nepionic leaf from the second to the seventh is shown in Plate III. The left and right sides of the figure show the extreme range of form found in each leaf. The index figures at the left-hand side of the plate indicate the position of the leaves with reference to the cotyledons.

Form of leaf.	Position of leaf.							
	1	2	3	4	5	6	7	8
(a) Five-lobed.....	19.5	.....	.....	.....	.....	.....	.....	.....
(b) Three-lobed.....	19.4	.....	.....	1.6	.....	.....	.....	.....
(c) Three-lobed.....	28.2	15.7	23.7	22.6	4.3	3.4	.....	.....
(d) Half 3-lobed.....	15.3	18.2	22.0	14.5	4.3	6.9	.....	.....
(e) Unlobed or irregular	25.0	61.2	39.0	22.6	17.0	3.4	.....	.....
(f) One pair of leaflets..	1.6	5.0	15.3	38.7	72.3	44.8	27.0	9.1
(g) Two pairs of leaflets	.....	.....	.....	.....	2.1	41.4	51.4	18.2
(h) Three pairs of leaflets	.....	.....	.....	.....	.....	.....	21.6	72.7



If the several categories into which these leaves have been divided are examined critically, the following facts will be noted:

1. They are not all of equal value. The second category (*b*) is only a special case of the third (*c*). The fourth (*d*) is transitional between (*c*) and (*e*). The fifth (*e*) is composite, but not readily divisible.

2. Some of the distinctions are qualitative, *i. e.*, complexly quantitative, as exemplified by (*b*), (*c*), (*e*), etc.; others are simply quantitative, as, for example, (*f*), (*g*), and (*h*).

3. They are not arranged in a logical linear series and are incapable of being so arranged. They have been arranged in the order in which they become dominant during development and without reference to their logical relations. The undivided or irregularly cleft blade so characteristic of the second nepionic leaf is the logical termination of a line of development from the 3-parted leaf through the half 3-parted, but the pinnate leaf with one pair of lateral leaflets, instead of joining directly to this undivided form which it follows, also comes logically from the 3-parted type. If the progress of the phylogeny of the species is correctly indicated by this ontogenetic series it would appear that after a gradual departure from the ancestral tripartite leaf to the undivided leaf there had been a sudden jump or mutation to the opposite extreme in which the clefts of the tripartite leaf became so exaggerated as to leave the lateral lobes separated from the terminal by a space, thus forming a pinnate leaf. It can not rightly be either affirmed or denied that such mutation took place in the history of the species, but it appears to me that any attempt to interpret the details of ontogenetic development as corresponding so definitely to phylogenetic development would be pressing the analogy to a wholly unwarranted degree.

In fig. 1 the variation in the several nepionic leaves from the first to the eighth is represented graphically in the form of curves, the several categories being treated as if of equal value. Although, as we have just seen, this is not strictly true, the figure still allows the derivation of at least one interesting conclusion—there is a progressive lessening of the variability from the first leaf onward. The modal class in the first nepionic leaf contained only 28.2 per cent of the individuals, or, if we should include in this class the special form of 3-parted leaf which has been separated as a distinct category, it would still contain only 47.6 per cent of the individuals, while the modal class in the eighth leaf included nearly 73 per cent of the specimens, and the variability within the class was very much less in the latter than in the former.

There are several ways in which we may account for the great variability in the earliest leaf and the decreasing variation with subsequent

development. If these juvenile leaves do correspond with adult conditions of the past we might suppose that at the time when the species was characterized by a tripartite leaf it was much more variable than it became later, and that the process of evolution acted to give it gradually a more and more fixed character. Or, on the other hand, it might be supposed that the species has been at all times about equally variable, but that by the "law of acceleration" the first nepionic leaf represents a much longer period in the history of the species than does any subsequent leaf. Again, it may be that these leaf-forms are not atavistic, and

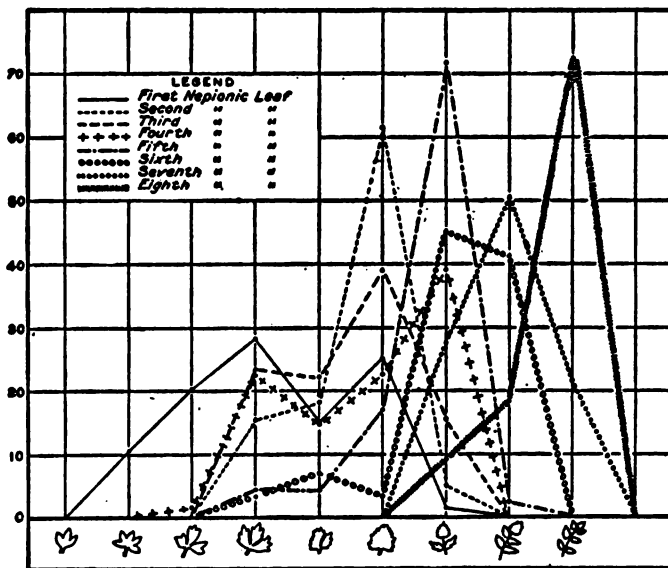


FIG. 1.—Graphic representation of the variation in the several "nepionic" leaves of *Sium cicutaeifolium*, from the first to the eighth, inclusive. Ordinates given in per cents.

the wider range of variation may merely represent a greater sensitivity to minute variations of the internal and external environment. As the plant becomes more and more firmly established it becomes morphologically more self-determinative. In other words, the greater variability and the gradual decrease in variability may be purely physiological facts unrelated in any direct way to the phylogenetic history of the species. It is possible indeed that each of these propositions may represent a partial truth, as they are not mutually exclusive. The species may have been more variable in its adult leaf-form, the law of acceleration may give rise to a greater range of atavistic variation in the earlier

leaves, and physiological causes may determine which atavistic form shall appear and may in addition give rise to forms or details of form which are in no sense atavistic.

A point in favor of the interpretation of the tripartite leaf as being at least in a general way atavistic may be found in the fact that ternate division of leaves is notably prevalent among the Umbelliferae; but it should not be forgotten that a ternate condition is a necessary logical transitional stage between any "simple" leaf and a pinnate leaf, and its significance must rest solely upon this logical relation. To show how gratuitous is any attempt to draw from the juvenile leaves conclusions regarding the leaf-form in ancestral groups it is only necessary to investigate the conditions found in the few instances in which the ancestry of a species is definitely known. Through the kindness of Dr. D. T. MacDougal, of the New York Botanical Garden, I am enabled to present photographs of the seedlings and adult rosettes of *Onagra lamarckiana* and *O. rubrinervis*, the former species being the parent of the latter. They represent the closest relationship possible between two species, and yet those who are experienced in their culture separate them with unflinching accuracy in the earliest juvenile stages. A comparison of the seedlings and the adults in Plates IV to VI makes evident the fact that the seedling of *Onagra rubrinervis* resembles much more closely the adult condition of the same species than either the seedling or the adult condition of its parent species, *Onagra lamarckiana*.

Turning now to other regions which have been supposed to present ancestral types, particularly to the two regions most strongly exploited by Cushman (1902, 1903, 1904) in his recent papers in the American Naturalist, we find conditions which are totally different from those we have just considered in the juvenile stages. The first of these regions is that at which a perennial herb resumes growth in the spring after hibernation. At the close of the first season from seed the leaflets of *Sium cicutaefolium* become more or less dissected into narrow segments, as shown in fig. 2. This modification is very often apparently related to the more aquatic condition of the habitat, and is in line with modifications in many other species whose dissected leaves appear to be correlated in some way with aquatic conditions; but it can be shown that this change in the form of the leaf of *Sium* takes place, though less perfectly, when the plants are not supplied with an unusual quantity of water. Plants taken up as seedlings in June and grown under mesophytic conditions in the window of a laboratory at the University of Chicago and later in the conservatory of the same showed dissection of the leaves similar to that exhibited by plants that were submerged in imitation of the effects of autumn rains.

PLATE IV.



Seedlings of *Onagra lamarckiana*, grown at the New York Botanical Garden.  
Photograph supplied by Dr. D. T. MacDougal.

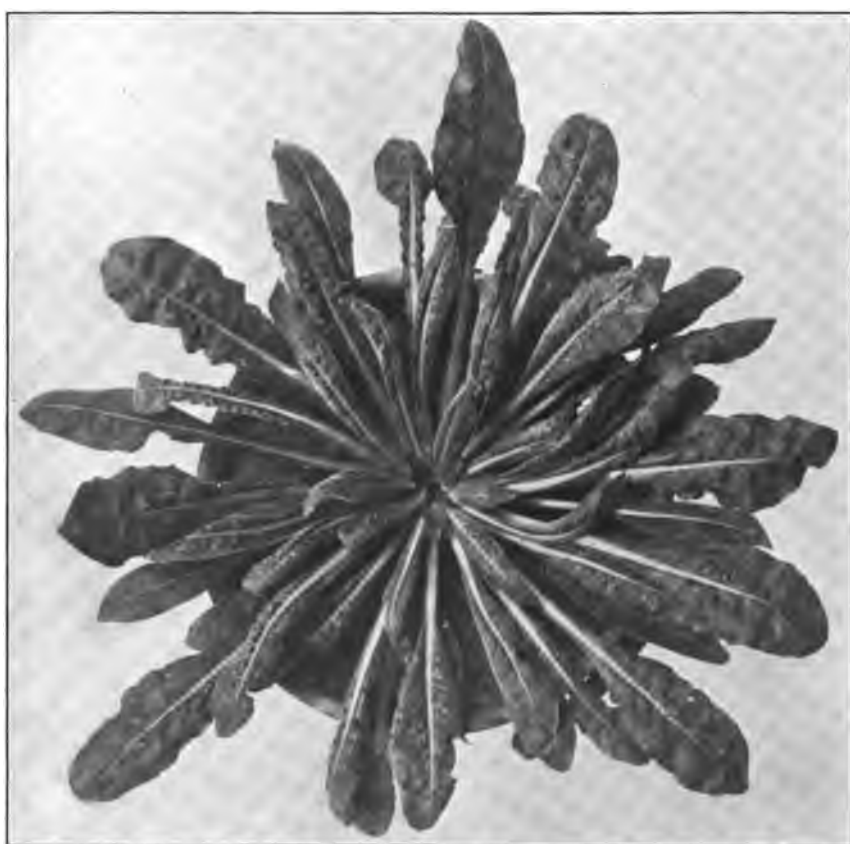
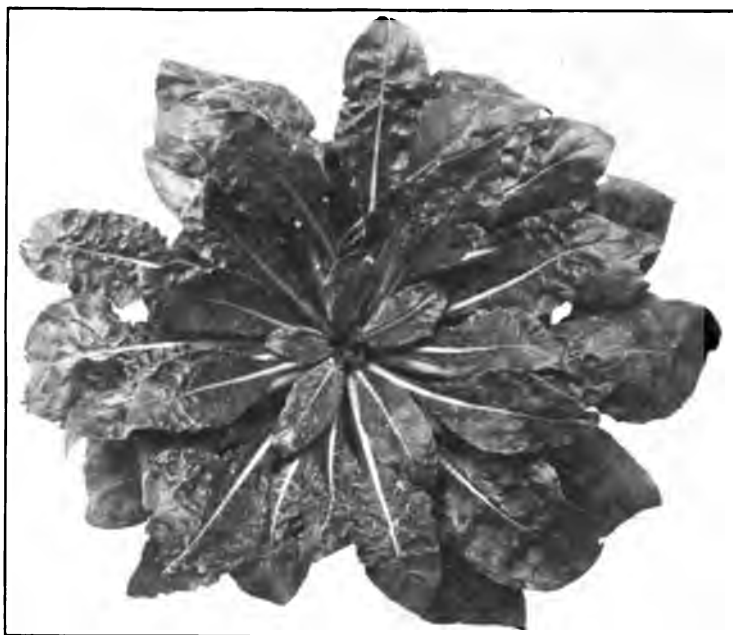




PLATE V.



Seedlings of *Onagra rubrinervis* grown at the New York Botanical Garden.  
Photograph supplied by Dr. D. T. MacDougal.



Large rosettes of *Onagra lamarckiana* (upper) and *O. rubrinervis* (lower), grown at the New York Botanical Garden. Photographs supplied by Dr. D. T. MacDougal.





Burns (1904) has recently demonstrated a similar independence from aquatic conditions, in the dissected leaf of *Proserpinaca palustris*, though McCallum (1902) had looked upon it as a direct response to the dilution of the protoplasm brought about by the abundance of water and the stoppage of transpiration. Burns considers the dissected leaf of *Proserpinaca* as a juvenile type, but this is certainly not the case in *Sium cicutaeifolium*.

A more pronounced, even extreme, dissection of the leaves characterizes the resumption of growth in the spring (Plates I and VII), so that

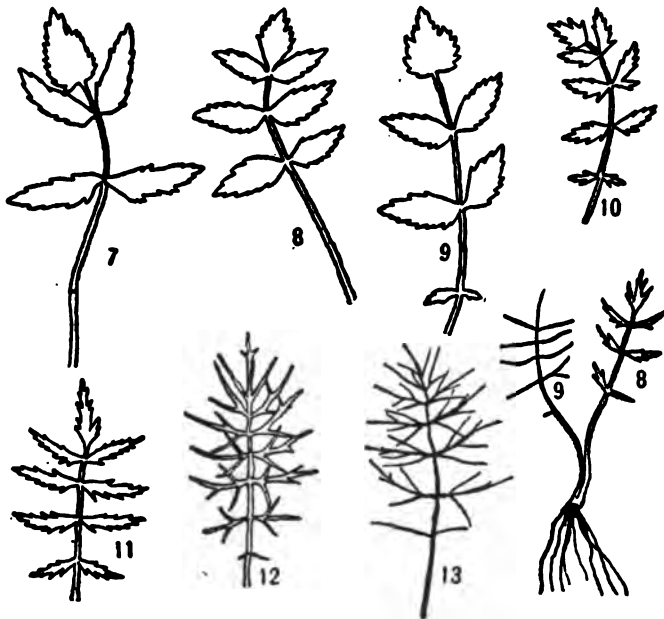


FIG. 2.—Autumnal modification of leaves in the seedlings of *Sium cicutaeifolium*. Numbers represent the position of each leaf in the series, beginning with the first neplonic leaf. Three-fourths natural size.

in so far as this region indicates the ancestry of the species the ancient *Siums* should have resembled a fennel (*Foeniculum*) or a parsley (*Lomatium*). These dissected leaves are rarely seen by the systematist who works only with pressed material, as one may convince himself by looking through the specimens of *Sium* in any large herbarium. Of more than 100 specimens of this genus in the herbarium of the New York Botanical Garden not one showed these dissected leaves. The change from dissected leaves to the simply pinnate leaves with linear, lanceolate

or lance-ovate, sharply serrated leaflets characteristic of the typical leaf of the stem, is very sudden (see Plates I and VII), and would again indicate a remarkable mutation if the course or ontogenetic development agrees with the phylogenetic.

In fairness to Cushman it should be said that while this discussion of the early spring growth is based on a literal interpretation of his papers, it evidently misrepresents his intention. The condition in *Sium* is analogous to that in the rosette plants, in which the writer had to look carefully beneath the rosette to find the "primitive" leaves. If he had examined the rosettes at some time during the preceding summer or autumn, when they were just beginning to develop, he would have found less difficulty in securing the leaves for which he was looking. The dissected leaves in old specimens of *Sium* result from the rejuvenation of axillary buds at the base of the flowering stem, and it will be seen later that the first leaves of these buds were of a more juvenile type, but that they belong to the autumn growth instead of the period of renewed vegetative activity in the spring.

When we examine the senescent stages approaching the inflorescence a series of forms is found entirely different from either of those already considered, and yet according to Cushman it is in the region of the inflorescence that we should be able to trace phylogeny to its earliest stages. During senescence the leaves of *Sium cicutaefolium* present a marked contrast in every particular to the juvenile stages. The progressive changes (fig. 3) present a simple linear series instead of the complex series seen in the seedlings, and there is an increasing constancy of form as senescence progresses instead of the increasing variability which should be expected if the senescent stages repeat the same story as that told by the juvenile stages, but in inverse order. Thus in 34 adult plants examined with reference to this point the second leaf below the principal inflorescence ( $n-4$ , figs. 3 and 6) had three pairs of leaflets in 10 per cent, two pairs in 56 per cent, and one pair in 34 per cent; the leaf subtending the primary umbel ( $n-3$ ) had one pair of leaflets in more than 70 per cent; and the peduncle arising axillary to this highest leaf of the principal axis bore a bract ( $n-2$ ) having a single lance-linear blade in over 80 per cent. In vigorous plants peduncles of tertiary or still higher orders occur, and the bracts ( $n-1$  and  $n$ ) on these show a regular reduction from the form just described as predominant on the secondary peduncles to small awl-shaped structures which apparently correspond to the base of the petiole and leaf-sheath of the earlier stem-leaves, the blade having completely disappeared.

Besides these differences in form between the senescent and the juvenile leaves, there is quite as marked difference in the texture, venation, etc. The dissected leaf has already been spoken of as having a form not rarely associated with aquatic habitats. Similarly the juvenile and senescent leaves have forms and textures usually associated with mesophytic and xerophytic habitats, respectively, the reduction of the blade, firm texture, and strong cuticularization of the stem-leaves being in marked contrast with the broad blades and delicate texture of the juvenile leaves. It will not be surprising to find that each of these three

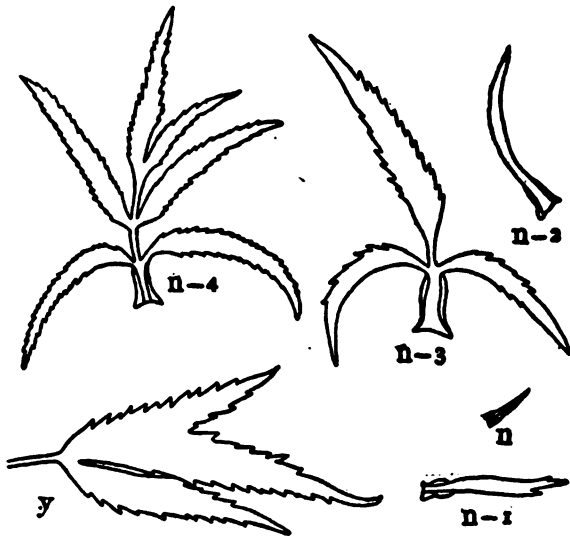


FIG. 8.—The senescent series of leaf-forms in *Sium cicutaeifolium*. Numbered downward from *n*, the most reduced leaf found in the inflorescence; *y* a terminal leaflet showing incomplete differentiation of a pair of lateral leaflets. Two-thirds natural size.

types of leaves is associated with just the conditions of environment to which it would appear to be adapted. The seedling develops in the shade of other plants during the summer, when the substratum is less wet; the dissected leaves occur in autumn and spring, when the favorite habitats of the plant are apt to be supersaturated or flooded with water; and the stem-leaves are raised above the substratum, where they are more exposed to the drying influences of wind, light, etc., and at the same time farther from their water-supply.

But too much stress can easily be placed upon external appearance as evidence of adaptation, and the dissected leaves, which suggest by their form an adaptation to hydrophytic conditions, do not bear out the suggestion when put to the test. They are unable to do sufficient pho-

tosynthetic work when submerged to allow the plant to continue its growth, and death speedily follows complete submergence. It might be assumed that the dissection is a *product* of the environment instead of an adaptation to it, and the apparent correlation of these three stages of *Sium* with different environmental conditions would accord well with the contention of Klebs (1903) and others that external factors are directly determinative of the form and activities of plants. But the plants which appear to demonstrate this proposition are quite exceptional. In *Sium cicutaeifolium* this direct relation between the form and the environment proves to be only apparent, and this species seems to agree with the vast majority of plants in presenting a rather definite cycle of development which it passes through whenever the environment supplies conditions which are favorable to growth. In such cases the environment is only indirectly determinative of vegetative activities. It supplies the energy, but the mechanism of the protoplasm determines what shall be the product, just as the muscles of the hand and arm used

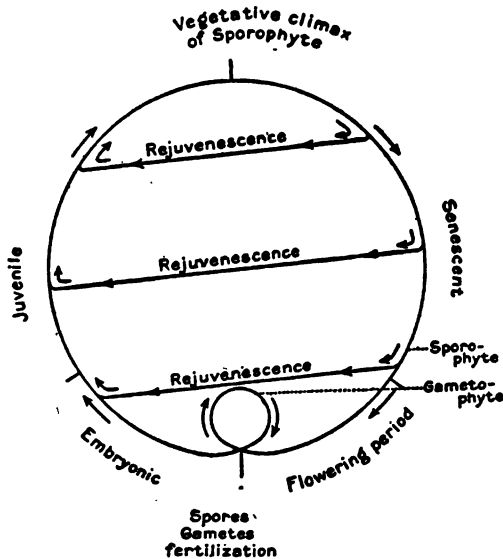


FIG. 4.—Diagram of the life-cycle of a spermatophyte, showing the relation of the process of rejuvenescence as a "short-cut" across the cycle. Upper "rejuvenescence" line may represent the rejuvenescence of buds at base of stem (fig. 7); the lower, the proliferations of the flower-buds (figs. 8 and 9).

in winding a clock supply the power which is converted by the peculiar mechanism of the clock into movement of the hands, ticking of the escapement, and striking of the hour.

When a cycle of vegetative activity comes to a close with the senescent stages it can be repeated only as a result of some process of rejuvenescence. Fertilization and seed production are to be looked upon as preparatory to or part of the most common process of rejuvenescence, as was pointed out long ago by Alexander Braun (1851), but this is not the only manner in

tinues the cycle on to the close of the senescent series, beginning at or slightly in advance of the stage attained by the axis at the level from which the bud springs. But when it fails to develop at once it can not

resume activity except through a process of rejuvenescence, which throws its development back to some earlier point in the cycle, and always at least as far down the juvenile side of the

cycle as the origin of the bud is down the senescent side, a relation which is clearly indicated by the slant of the "rejuvenescence" lines in the diagram (fig. 4).

It is this less differentiated, juvenile condition which usually occurs when a resting bud is reawakened into active development which suggested to Jackson (1899) his conception of localized stages having phylogenetic significance.

Some cases of rejuvenescence were observed in a specimen of *Sium cicutae-folium* which had been torn up by the roots and thrown down in such a way as to submerge the upper portion of the stem and the immature inflorescence. The axillary buds

of the upper part of the stem, which might otherwise have produced secondary branches of the inflorescence, and which would then have

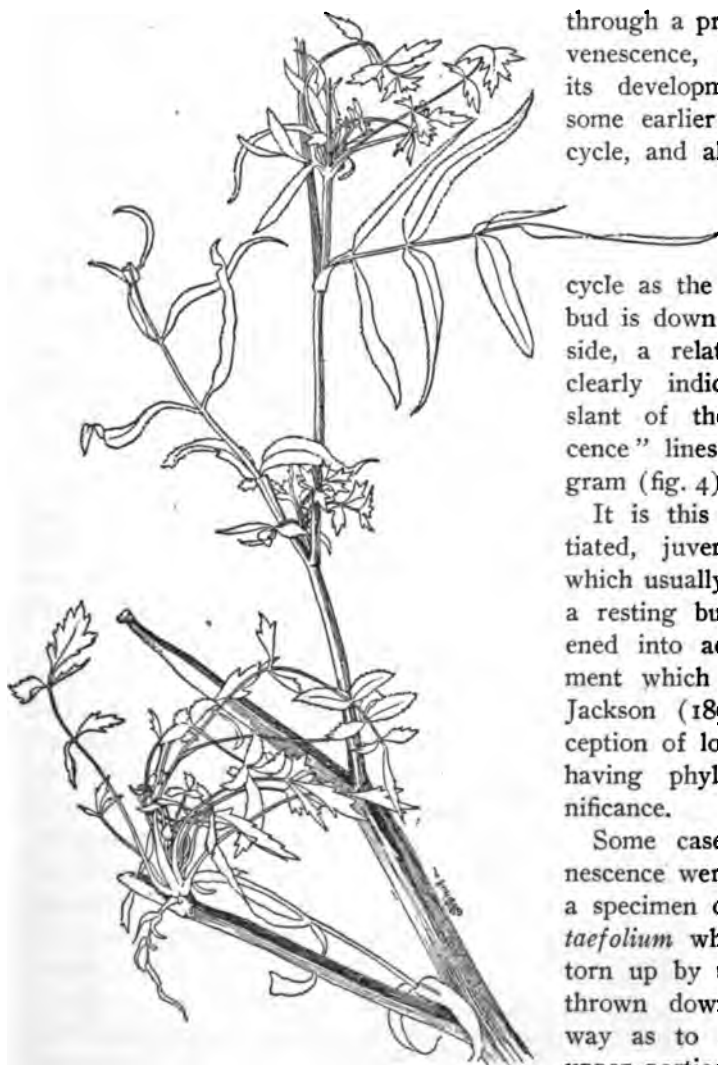


FIG. 5.—Part of the stem of a specimen of *Sium cicutae-folium* with three rejuvenated buds. Drawn by J. Marion Shull from a photograph.

borne only the closing members of the senescent series of leaf-forms (fig. 3), were rejuvenated as a result of the submergence and made to begin a new series, the early members of which show the most interesting transitions from the senescent to the juvenile forms. Two of these rejuvenations are shown in figs. 5 and 6. The two leaves (n-4, n-5)

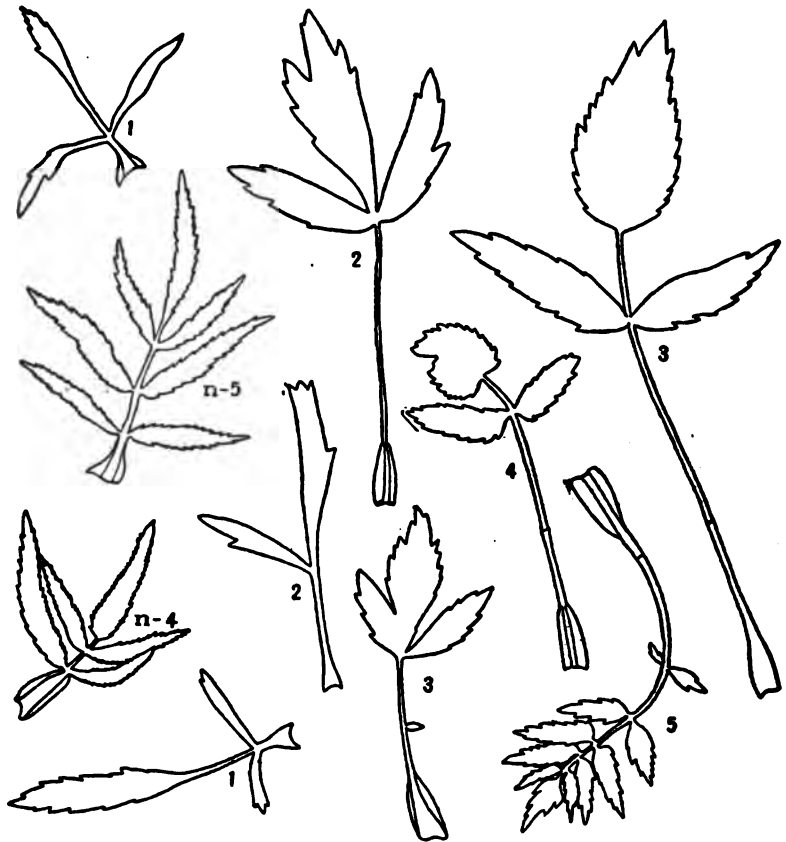


FIG. 6.—Two rejuvenated buds from the upper portion of a stem of *Sium cicutaeifolium*: n-5 and n-4, leaves to which the buds were axillary. Numbers represent the position of each leaf in the bud. Two-thirds natural size.

at the left in fig. 6 are the leaves to which the two rejuvenations shown in the same figure were axillary. Unrejuvenated, the first leaf produced by each of these buds would have been a pinnate leaf of exactly the same character as the leaf to which the bud was axillary, but with a less number of leaflets. Instead of this we see in each case a leaf having the same arrangement of parts, to be sure, but greatly modified in



*Sium cicutaefolium* Gmel. The first four leaves of the spring-growth of an old specimen. Two-fifths natural size. Photographed April, 1905, from a specimen taken into the house February 25, 1905.





the direction of the tripartite leaf, which will be recalled as the modal condition in the first nepionic leaf. In the second leaf in the one case a form similarly transitional to the half-tripartite leaf occurred, and in the other case the juvenile type of 3-lobed leaf was perfected. With the third leaf in the one rejuvenation and the fourth in the other, a pinnate form was produced which corresponded in every way with that seen above to be the modal condition of the fifth nepionic leaf. This was as far as one of these rejuvenations was followed. In the other the fifth leaf had five pairs of leaflets, a degree of differentiation not

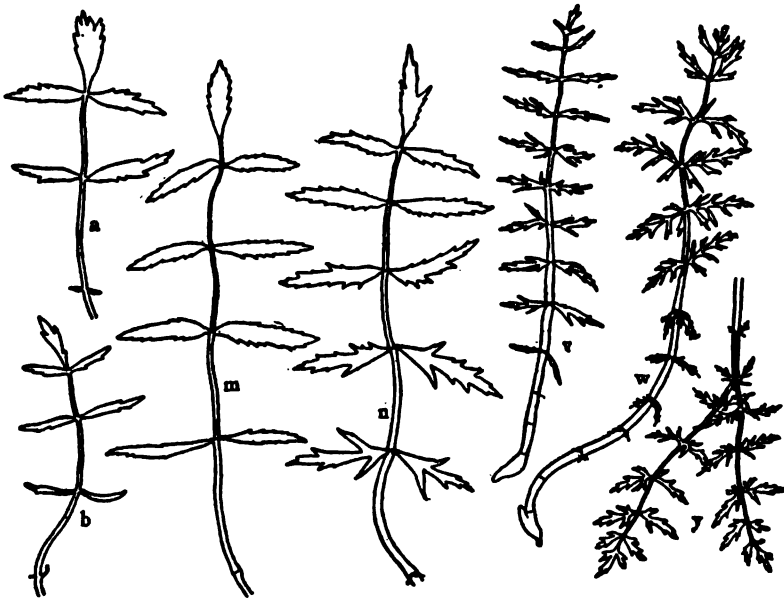


FIG. 7.—Leaves of a rejuvenated bud from near the base of a stem of *Sium cicutae-folium*. Letters represent in a general way the position of each leaf in the rejuvenation; y, an abnormally divided blade. Four-ninths natural size.

usually attained during the first year from seed. Later these rejuvenations produced the dissected leaves characteristic of the autumn and early spring growth.

Lateral buds at the base of the flowering stems are regularly rejuvenated in the autumn, and the first leaves are pinnate with one or several pairs of undivided leaflets and are followed by a linear series leading more or less quickly to the dissected condition (fig. 7). It will be noted that these basal rejuvenations never present leaves suggestive of the earliest juvenile stages, as is the case in the rejuvenescence of buds

near the inflorescence, probably because their senescence has not progressed so far.

Senescence reaches its culmination in the region of the flower. Remarkably interesting conditions were found in the inflorescence men-

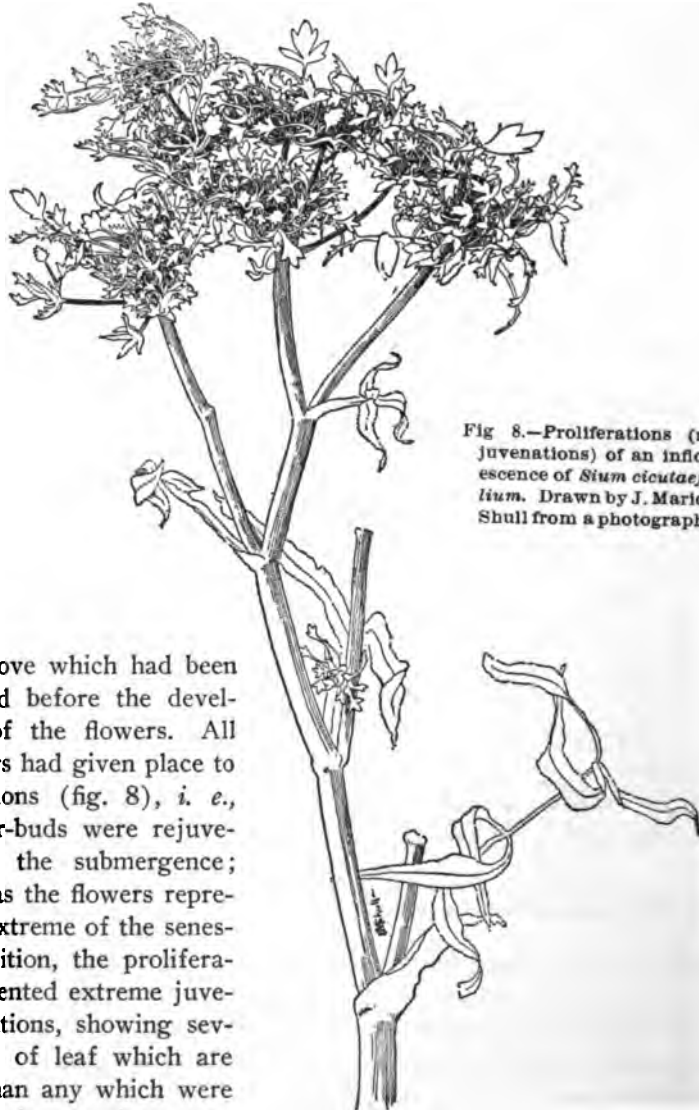


Fig 8.—Proliferations (rejuvenations) of an inflorescence of *Sium cicutae-folium*. Drawn by J. Marion Shull from a photograph.

tioned above which had been submerged before the development of the flowers. All the flowers had given place to proliferations (fig. 8), i. e., the flower-buds were rejuvenated by the submergence; and just as the flowers represent the extreme of the senescent condition, the proliferations presented extreme juvenile conditions, showing several types of leaf which are simpler than any which were found in the seedlings, and usually reaching the condition of the first nepionic leaf at the third or fourth leaf of the proliferation. Some of the proliferations were more

precocious than this, however, and all showed a much more rapid development of the dissected form than is seen in the seedling.

The simplest leaf presented by these proliferations (fig. 9) was a minute oblong undivided structure which might be slightly widened and flattened in the distal half, but otherwise showed no distinction of blade and petiole. This might be followed by another undivided leaf



FIG. 9.—Proliferations from an inflorescence of *Sium cicutaeifolium*. Numbers show position of each leaf in its own proliferation. Various magnified,  $\times 5$  to  $\times 8$ .

with a wider, elliptic blade. Then there might be a leaf having one or a pair of simple lateral lobes, followed perhaps by the 5-lobed leaf or the form which has been described as the simplest type of 3-lobed leaf occurring in the seedling, having a 2-notched terminal lobe and bifid lateral lobes. Whether the juvenile stages are atavistic or not, these early leaves of the proliferations logically precede and lead up to them, and carry us down the series to the simplest possible type of leaf.

The rejuvenescence of all these buds as the result of a change from an aerial to an aquatic habitat is in perfect agreement with Burns's (1904) interpretation of the changes induced in a similar way in *Proserpinaca palustris* and very greatly strengthens his position. The fact that the juvenile leaves of that species are finely dissected in the manner so frequently found in the climactic or ephebolic stages of typical submerged plants is either purely a coincidence or may be related in some unknown way to the past environmental relations of the species, as suggested by Goebel (1899-1901, p. 546). In *Sium*, where the juvenile leaf is not at all of the hydrophytic type, submergence in water does not produce a dissected, hydrophytic leaf, but the mesophytic form of leaf characteristic of the *Sium* seedling.

This change of view regarding the effect of water in producing the modified leaf-form of these plants does not detract in the least from the value of the negative results of McCallum's (1902) investigation into the nature of the stimulus involved, but gives those results a bearing on the phenomenon of rejuvenescence instead of the change from a terrestrial to an aquatic type of leaf. To ascribe a phenomenon to good or poor vegetative conditions (Burns, 1904, p. 586) does not yet trace it very near to its ultimate cause or causes, but perhaps is as definite as the present state of our knowledge regarding rejuvenescence would warrant. The great vigor of the rejuvenated buds in *Sium* is scarcely consistent with the view that they are due to starvation or any other poor vegetative conditions, and, indeed, when we find flower-buds, representing as they do the low ebb of vegetative vigor, suddenly awakened into a new cycle of vegetative development we should assume that they have found good rather than poor vegetative conditions.

It is evident that a distinction must be made here between the cause of rejuvenescence or the reawakening into the ascending side of the vegetative cycle and the cause which determines just what point in the cycle shall be attained in any specific case. I would offer the tentative suggestions, (a) that a process of senescence resulting in a checking or a cessation of growth is a necessary condition antecedent to rejuvenescence, and (b) that the cause of the reawakening may be due to either or both of two complex factors, namely, an increase in available food-equivalent and an increased lability or mobility (perhaps largely fluidity) of the protoplasmic substances. The former may be predominantly operative when lateral buds are forced into development by checking the growth of a terminal bud, and the latter may be the dominant factor in cases of submergence. (c) The causes which determine the point in the cycle which shall be attained under any specific condi-

tion may well be the relative degree of one or other of these factors or of their resultant, as compared with that necessary for the production of the climax type of leaf of the adult plant. This is essentially in accord with Burns's (1904, p. 586) suggestion of poor vegetative conditions, and also with the earlier observations of Cushman (1902, p. 885) that weak individuals and those growing on poor soil or with insufficient moisture present earlier stages than do more vigorous specimens or those growing under more favorable conditions with respect to soil and water-supply. As applied to *Proserpinaca* this would mean that the juvenile type of leaf in the submerged plant is primarily the result of protoplasmic dilution, but that the failure to attain the adult condition is due to less favorable relations as to food-supply. Ordinarily in submerged plants of *Proserpinaca* these two factors may be conceived to balance each other in such a way as to produce the dissected leaf continuously, but an unusually vigorous plant may be able to provide a food-supply sufficient to overbalance the effect of dilution, and so give rise to the adult type of leaf which is occasionally seen even in submerged plants. When the dissected leaf is produced in aerial parts it is primarily due to a condition as to food supply better than that available in the resting condition, but not equal to that necessary for the production of the adult leaf-type. With the return of spring, conditions for food-manufacture are improved and the adult leaf appears at once.

An explanation of senescence in the same terms would ascribe it to decreasing lability or fluidity unaccompanied by a compensatory increase in the available food-equivalent—a condition coming just as fully under the head of poor vegetative conditions as does that producing the juvenile stages.

Not only are different regions of the axis supposed to bear leaves characteristic of different periods in the history of the species, but it is maintained by both Jackson (1899) and Cushman (1902, 1903) that certain parts of the leaf, especially the apical region, likewise show atavistic conditions. Leaving wholly aside for the present the relation between the parts of the present adult leaf and the form of the ancestral leaf, the question involved in this proposition is the localization of the differentiative activities in the leaf. The simpler character of the apical region in many leaves is undeniable, and it may correspond in certain cases, therefore, with ancestral conditions, though this has not been proved in any specific case. But the simplicity of the apical region has led both of these writers into error when they conclude that new characters arise at the base of the leaf. After examining many leaves and

also the figures upon which Jackson and Cushman base their conclusions, I am convinced that with possible rare exceptions the new character added to a leaf having a single blade and an entire margin consists in an indentation or an incision rather than an outgrowth, and that, in general, increased complexity is brought about by an increasing number and depth of these incisions, which do not and can not occur *at* the base, but must occur *above* it. That part of the base below the lowest incision is characterized by an entire margin and is "primitive," therefore, in the same sense as is that part of the apex above the highest incision. Just as Cushman (1903, p. 244) noted that emarginate apices may develop from acute ones in *Astragalus adsurgens*, so in cases like that of his *Arabis albidia*, in which truncate and cordate bases occur in a series beginning with attenuate bases, these forms are late modifications of a tapering base, due to the excess of marginal growth as compared with that of the mid-rib. Although the basal margin is thus distorted from its original direction, it retains its unbroken "primitive" character.

The figures which illustrate Cushman's papers show these facts so clearly that it seems strange that he should not have recognized them. Particularly in *Sibbaldiopsis* (*Potentilla*) *tridenata*, *Artemisia stelleriana*, and *Sanguisorba* (*Poterium*) *canadensis* is it difficult to harmonize his figures with his statement that new characters are produced at base. In the first two of these plants the new character, as I under-

stand it, consists in the appearance of two small indentations very near the apex. In *Sanguisorba canadensis* the leaf is pinnate, and in the later stages of the senescent series each proximal leaflet presents in each leaf a peculiar inequilateral form, though the number of leaflets de-

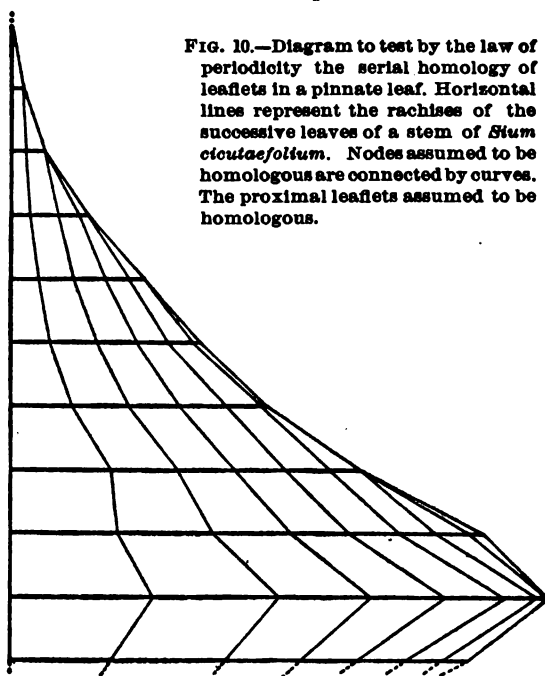


FIG. 10.—Diagram to test by the law of periodicity the serial homology of leaflets in a pinnate leaf. Horizontal lines represent the rachises of the successive leaves of a stem of *Sium cicutaeifolium*. Nodes assumed to be homologous are connected by curves. The proximal leaflets assumed to be homologous.

creases regularly as the inflorescence is approached. In order to make this leaf fit his view of basal differentiation, Cushman (1903, p. 254) assumes that as each proximal leaflet disappears the next higher leaflet takes on this same inequilateral form.

According to this view the proximal leaflets are the newest. If, on the other hand, it be conceived that the leaflets appear in apical succession by the division of the terminal leaflet, and that they disappear through the loss of one pair of incisions after another, proceeding now basipetally, the proximal leaflets, which have in every late senescent leaf the same peculiar shape, will be the oldest instead of the newest, and the inequilateral leaflets of one leaf will be homologous with those of all of the other leaves. In the latter case it would occasion no surprise to find that these leaflets show a well-established form which occurs with considerable constancy in each succeeding leaf. If these proximal leaflets were in a state of perpetual nascence and evanescence we would expect the process to result in frequent imperfect or incom-

plete differentiations and consequent great variation, a condition never realized.

Every one will recall frequent instances in which the terminal leaflet of a pinnate leaf showed imperfect formation of lateral leaflets by incisions of greater or less depth near its base ( $n=4$  and  $y$ , fig. 3), and every degree of division will have been noted, from a slight notch to the complete formation of a pair of adjacent leaflets. This ap-

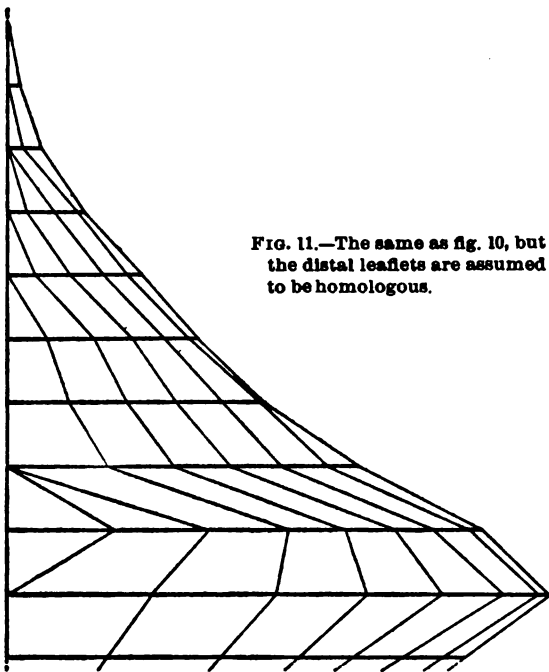


FIG. 11.—The same as fig. 10, but the distal leaflets are assumed to be homologous.

pears to me to be the best possible evidence that in this region, just above the base of the terminal leaflet, is the place of progressive differentiation and reintegration in pinnate leaves, and that it is here and not in the proximal leaflets that new characters are to be looked for.



As further evidence that this is the correct interpretation of the pinnate leaf, the diagrams shown in figs. 10 and 11 were constructed as follows: All the leaves of a single stem of *Sium cicutaefolium* (omitting several which had disappeared at the base) were arranged in their normal sequence, but side by side, with their rachises parallel and at equal intervals. These rachises are represented by the horizontal lines of the figures. The point of origin of each pair of leaflets was then marked, and the figures were completed by connecting with lines the points of origin of leaflets assumed to be homologous. In fig. 10 the proximal leaflets, and in fig. 11 the distal leaflets, are assumed to be homologous. The basis for the interpretation of these figures is to be found in the demonstration by Fräulein Tammes (1903) that the law of periodicity underlies all morphological phenomena in such a way that serially homologous characters increase regularly to a maximum and then decrease, decrease regularly to a minimum and then increase, or that they form a half period, *i. e.*, they begin with the maximum and end with the minimum, or *vice versa*. Even a most superficial inspection of the two figures discloses the fact that in one there is a simple underlying law which would lend itself to ready formulation, while in the other all is confusion. The characters which are represented in these figures are the interfoliola or portions of the rachis between successive pairs of leaflets. Homologous interfoliola are represented by the portions of the horizontal lines included between any two consecutive curves. In fig. 10 these interfoliola are seen to reach a definite maximum length in the second leaf from the base of the figure and to diminish continuously from that maximum upward until each in turn is reduced to zero, as required by the law of periodicity. The only irregularities appear in the two distal interfoliola of the third leaf from the base of the figure and in the distal interfoliolium of the first and of the fifth leaves from the base, these variations in the distal interfoliola being in full accord with my view that this is the region of active differentiation and reintegration in the leaf. In fig. 11, on the other hand, there is not a single instance in which a series of interfoliola assumed to be homologous shows an increase to a definite maximum followed by a continuous decrease. The law of periodicity is beautifully exemplified in fig. 10, which is based on the assumption that the proximal leaflets of one leaf are homologous with the proximal leaflets of every other leaf of the same stem, while there is no indication of that law in fig. 11, in which the distal leaflets are assumed to be homologous. Certainly no more conclusive proof of the truth of my proposition could be asked.

As in the case of the juvenile and senescent leaves, the sole basis for the assumption that the base and apex of a leaf exhibit conditions which

were characteristic of the whole adult leaf at some time in the past history of the species is the fact of their greater simplicity. The relation is purely a logical one, and the condition of these regions of the leaf are not unlikely to disagree with phylogenetic conditions in every detail except simplicity.

Although this study makes it evident that no satisfactory inferences can be drawn from the forms occurring at various ontogenetic stages regarding the ancestral adult conditions, these forms do have a bearing upon the relationship of allied species. The similarity of two species as to the characters possessed at any of these stages would lend evidence in favor of their close relationship in the same way that similarity in any other activity or character would, not because of resemblance to a common ancestral adult condition, but because of the presumptive evidence of similarity in present protoplasmic structure.

All the evidence now available indicates that when specific differentiation takes place the changed structure of the protoplasm which produces new adult characters also gives rise to new characters in the juvenile and senescent series. The assumption that these stages have a phylogenetic significance tends to obscure the fact that they are the results of present conditions instead of the past history of the protoplasm and that they are in need of physiological rather than phylogenetic investigation and interpretation.

## SUMMARY.

The various forms of leaf which occur at different parts of a specimen of *Sium cicutaeifolium* are described and their bearing on the phylogenetic history of the species is considered. The principal conclusions are as follows:

There is great variability in the early nepionic leaves, the first leaf being the most variable and the variability being progressively lessened in subsequent growth.

The interpolation of an undivided leaf between the 3-lobed and the pinnate leaf is illogical and might be interpreted as representing phylogenetic mutation.

To show how wholly gratuitous is the attempt to draw conclusions from juvenile stages regarding ancestral adult conditions, it is pointed out that in the species of *Onagra*, where the ancestry is definitely known, the juvenile leaves may resemble more closely the adult leaves of the same species than they do either the seedling or the adult leaves of the parent species.

The senescent stages are totally different from those of the seedling. The leaves show a regular reduction without sudden changes of type, and there is increasing constancy in form as higher stages are reached.

Although the several stages of *Sium* present the appearance of being closely correlated with the successive changes in its environment, the plant passes through the same stages whenever the conditions are favorable for growth, regardless of the characteristics in the environment which have been supposed to determine the several types of structure.

This cycle of development can be repeated only through rejuvenescence. This may result from fertilization and seed-production, but can be brought about in other ways. Rejuvenations of axillary buds and of flower-buds are figured and described. Rejuvenescence in these buds was caused by submergence in water of stems in the senescent state. The later the stage of senescence reached the earlier are the juvenile stages produced on rejuvenescence. Proliferations of flower-buds showed several leaf-forms which are simpler than any found in the seedlings.

Rejuvenescence may be due to increased available food-equivalent, or to increased lability or fluidity of the protoplasmic substances, or a combination of these two factors. The stage attained in any case of rejuvenescence may be due to the relative value of the resultant of these two complex factors, as compared with that necessary to the production of the climax type of leaf of the adult plant.

It has been claimed that the apex of a leaf presents primitive conditions and that new leaf-characters appear at the base of the blade. It is shown here that the base is also "primitive" and that the new characters appear above the base.

The proximal leaflets of pinnate leaves on the same stem are homologous, as are all other pairs of leaflets having positions of like order, counting from the proximal pair.

The sole basis for the assumption that localized stages present atavistic characters is the fact of their greater simplicity. No satisfactory inferences can be drawn from ontogenetic leaf-characters regarding the phylogenetic history of the species. The various stages are the result of present protoplasmic structure instead of the past history of the protoplasm, and a change of structure which results in new adult characters may also produce changed juvenile and senescent characters. They are in need of physiological instead of phylogenetic interpretation.

STATION FOR EXPERIMENTAL EVOLUTION,

COLD SPRING HARBOR, N. Y., *December, 1904.*

## LITERATURE CITED.

- AGASSIZ, LOUIS.  
1848-1849. Twelve lectures on comparative embryology. Boston: Lowell Institute.
- BRAUN, ALEXANDER.  
1851. Reflections on the phenomenon of rejuvenescence in nature, especially in the life and development of plants. Translation from the German, by A. Henfrey. London: Ray Society, 1853.
- BURNS, GEORGE P.  
1904. Heterophylly in *Proserpinaca palustris* L. Annals of Botany, 18: 579-587.
- CUSHMAN, JOSEPH A.  
1902. Studies of localized stages of growth in some common New England plants. Amer. Nat., 36: 865-885.  
1903. Studies of localized stages in some plants of the botanic gardens of Harvard University. Amer. Nat., 37: 243-259.  
1904. Localized stages in common roadside plants. Amer. Nat., 38: 819-832.
- GLASER, OTTO C.  
1902. The law of von Baer. Science, N. S., 15: 976-982.
- GOEBEL, KARL.  
1898-1901. Organographie der Pflanzen insbesondere der Archegoniaten und Samenpflanzen. pp. xviii, 838. Figs. 539. Jena: Gustav Fischer.
- HAECKEL, ERNST.  
1866. Generelle Morphologie der Organismen, 2 Bde. Berlin: G. Reimer.
- HYATT, ALPHEUS.  
1890. Genesis of the Arietidae. Smithsonian Contribution 673, and Mem. Mus. Comp. Zool., 16:  
1897. Cycle in the life of the individual (ontogeny) and in the evolution of its own group (phylogeny). Proc. Amer. Acad. Arts and Sciences, 32: 209-224.
- JACKSON, R. T.  
1899. Localized stages in development in plants and animals. Proc. Boston Soc. Nat. Hist., 5: 89-153.
- KLEBS, G.  
1903. Willkürliche Entwicklungsänderungen bei Pflanzen. pp. iv, 166. Figs. 28. Jena: Gustav Fischer.
- MCCALLUM, W. B.  
1902. On the nature of the stimulus causing the change of form and structure in *Proserpinaca palustris*. Bot. Gaz., 34: 93-108.
- TAMMES, Fräulein TINE.  
1903. Die Periodicität morphologischer Erscheinungen bei den Pflanzen. Verhandelingen d. Koninklijke Akad. v. Wetenschappen te Amsterdam, 9 (No. 5): 1-148.
- VON BAER, K. E.  
1828. Ueber Entwicklungsgeschichte der Thiere. Beobachtungen und Reflexion. Königsberg: Gebr. Bornträger.













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